EFFECTS OF AN INTENSE FIRE ON HEADWATER STREAMS OF THE COLVILLE NATIONAL FOREST, WA

By

Cassie Danielle Mellon

RECOMMENDED:

Advisory Committee Chair

Director, Fisheries Division

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

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THE EFFECTS OF INTENSE FIRE ON HEADWATER STREAMS OF THE COLVILLE NATIONAL FOREST, WA

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Cassie Danielle Mellon, B.S.

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Abstract

Forest fires play an important role in shaping ecosystems, and there has been growing concern on the effects of high intensity fires on forest and aquatic ecosystems. Headwater streams are highly connected to riparian and surrounding terrestrial systems, and to downstream aquatic systems, partly through prey and organic matter transfers via aquatic invertebrate drift and emergence. Because of their small size, headwater streams may experience the greatest initial impact from forest fire, but may also return to pre-fire conditions quicker than larger streams.

In this study, headwater streams from replicated burned and control watersheds were sampled in the two years following an intense forest fire in northeastern Washington. Benthic, drift and emergence samples of aquatic invertebrates were taken and analyzed for differences in density, biomass and community composition between watershed types. There was significantly higher density of invertebrates in burned sites, but no difference in biomass except in invertebrate emergence which was greater at burned sites. There was lower diversity in the burned watersheds, and the invertebrate community was dominated by chironomids. These changes in invertebrate density and community composition could influence the food resources available to aquatic and riparian consumers.

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Introduction

Forest fire plays an important role in shaping and defining ecosystems. Fire is a natural disturbance process, which many ecosystems, especially in the western U.S., rely on for regeneration and maintenance of diverse, productive habitats (Bisson et al. 2003; Minshall 2003). Due to the high connectivity between terrestrial and stream ecosystems, disturbance to the forest often also affects streams. Aquatic ecosystems have evolved to be resistant to or be able to recover from natural disturbances such as fire, although in systems with a history of management and anthropogenic disturbance, fire may have a greater effect (Bisson et al. 2003; Minshall 2003; Beschta et al. 2004). Post-fire management activities, such as salvage logging, grazing and seeding, may slow natural recovery processes by introducing non-native species, compacting soils and increasing risks of debris flows (Beschta et al. 2004; Karr et al. 2004). While we have a general understanding of how forest fire affects benthic invertebrate communities in relatively undisturbed ecosystems (Minshall 2003), we have little knowledge of the effects of fire in managed forests and the effects of fire on the connections between headwater streams and adjacent ecosystems as potentially demonstrated by invertebrate drift and emergence.

Forest fire effects on aquatic communities vary greatly by location and severity (Minshall 2003), but are greatest in small headwater streams with measurable effects decreasing as stream size increases (Minshall, Brock and Varley 1989). Fire has a stronger influence on headwater streams than large rivers because a greater proportion of the watershed is likely to be burned (Minshall, Robinson and Lawrence 1997) and the high stream margin to water volume ratio. As watershed area increases, there will be a

higher percent of unburned forest, and the riparian area is more likely to retain its function (Bisson et al. 2003; Dwire and Kauffman 2003; Minshall 2003). Loss of vegetation cover from fire or other disturbance can have a profound effect on aquatic resources (Piccolo and Wipfli 2002; Dwire and Kauffman 2003). Following loss of riparian vegetation to fire, streams are hypothesized to become autotrophic as increased sunlight increases primary production (Minshall et al. 1989). This shift from heterotrophy to autotrophy will likely cause a shift in dominant invertebrate functional feeding groups, from shredders that typically dominate headwater streams to filter feeders or collector-gatherers (Minshall et al. 1989). Additionally, there may be a shift from specialist to generalist feeders (Mihuc and Minshall 1995). Increased algal production may result in a trophic cascade of increased abundance of aquatic invertebrates, resulting in an increase in the food available to predators (Hawkins, Murphy and Anderson 1982). However, sediment loading, high temperatures, channel scouring, or other post-fire disturbance could greatly influence these shifts in and recovery time for invertebrate communities (Minshall 2003).

In addition to the predicted increases in primary productivity and the shift from heterotrophy to autotrophy, loss of riparian vegetation may increase erosion and overland flow (Murphy et al. 1986). This loss of stability may result in increased sedimentation and turbidity in headwater streams (Waters 1995), especially following intense summer thunderstorms that occur periodically in the western U.S. Post-fire water temperature may also increase due to loss of riparian canopy cover. Short term spikes in water

temperature during the fire may result in die offs of some fish and invertebrate species. Longer term increases may be harmful to species that were already temperature stressed.

Typically headwater streams are heterotrophic (Vannote et al. 1980), with the majority of food resources derived from outside the aquatic system (e.g., leaf litter inputs). The forest also provides the stream with shade, bank stability, habitat structure, and nutrients. Conversely, there is an important movement of food resources, in the form of invertebrates and detritus, from headwater streams to terrestrial and downstream ecosystems and between terrestrial and freshwater ecosystems (Nakano and Murakami 2001; Sabo and Power 2002; Wipfli and Gregovich 2002; Wipfli and Musslewhite 2004; Baxter, Fausch and Saunders 2005). Terrestrial insects falling into the stream provide food for fish and other aquatic predators (Wipfli 1997; Kawaguchi and Nakano 2001; Allan et al. 2003). Fishless headwater streams in turn provide detritus and invertebrates via drift to downstream, fish-bearing systems and through aquatic insects emerging into the riparian zone (Wipfli and Gregovich 2002). Emerging aquatic insects can be an important source of food to riparian area wildlife (e.g., birds, bats, amphibians and other insects) (Jackson and Fisher 1986; Power 2001; Sabo and Power 2002; Baxter et al. 2005). Invertebrate contribution to drift varies by species and may increase in response to stresses such as predation, lack of food or habitat, high sediment loads, or high temperature (Collier and Quinn 2003; Wipfli and Musslewhite 2004). The transfer of food and energy as invertebrates drift and emerge into new habitats can subsidize the foodwebs of adjacent ecosystems (Baxter et al. 2005). With changes in vegetation cover, sediment and water temperature following fire, there is likely to be a change in this

connectivity between aquatic and terrestrial systems and between headwater and downstream reaches.

Natural fire cycles vary from frequent, low intensity to less frequent but higher intensity fires depending on forest type and climate (Agee 1993). Recently there has been concern that a shift is occurring in these natural fire cycles to more frequent, large, high intensity fires (Bisson et al. 2003; Kauffman 2004; Williams and DellaSala 2004). Since 1960, the largest fire seasons have occurred in 2000, 2002 and 2005 and more than one billion dollars were spent fighting fires in 2000, 2002, and 2003 (www.nifc.gov). Although the largest recorded fire years have all been recent, there were large stand replacing fires prior to 1960 and prior to European settlement (Agee 1993). The apparent increase in acres burned may be due to an actual increase in forest fire or could be due to increased accuracy in reporting fires and amount of public land (Schoennagel, Veblen and Romme 2004). There is evidence that in some regions, especially in dry ponderosa pine ecosystems, this increase may be occurring due to fuels built up from previous fire suppression activities, forest management practices, or climate change (Moore, Covington and Fule 1999; Grissino-Mayer and Swetnam 2000). Studies have shown that in other regions, large fires such as the Yellowstone fires of 1988 are not outside the range of the natural fire cycle and were likely not greatly influenced by fuels buildup (Romme and Despain 1989; Schoennagel et al. 2004).

The fire history of the Colville National Forest, where this study was conducted, is similar in some respects to that of Yellowstone and the northern Rocky Mountains. There is a history of large, stand-replacing fire in this region with tree ring studies

showing a fire return interval of 400 years with a more frequent return interval likely (Daubenmire and Daubenmire 1968). Much of the Colville National Forest burned in the 1920's and 1930's resulting in present day stands of approximately 70-yr-old, small diameter, densely stocked timber. This study was conducted in the two years following the Togo Fire that burned 5000 acres in summer 2003. Whether the Togo Fire and the perceived increase in large, intense forest fires is part of natural fire cycles or impacted by management activities and climate change is uncertain. Regardless, fires will continue to occur and a better understanding of the effects on aquatic ecosystems is needed to manage fire for maintaining diverse, productive ecosystems.

There have been a number of studies on the effects of fire on aquatic ecosystems in the Rocky Mountain region. Work by Minshall et al. (1997) following the Yellowstone fires of 1988 showed little change in invertebrate density or biomass but there were shifts in functional feeding groups and an increase in Chironomidae and *Baetis* (Baetidae). A study in the Frank Church Wilderness of Idaho (Minshall et al. 2001b) showed increased biomass of invertebrates ten years post-fire, but no change in density. Many previous fire studies have been in wilderness areas or in areas with minimal human influence. It has been predicted that the effects of fire on aquatic ecosystems will be greater in areas with more human impacts such as logging, road building and grazing (Minshall 2003). Results from a study by Rinne (1996) in a managed forest in Arizona concur with this prediction, immediately following fire invertebrate densities sharply declined and remained reduced three years post-fire. Salvage logging can delay natural recovery of forest and riparian systems through increasing soil compaction, erosion, and slowing forest regeneration

following harvest and road building activities (Beschta et al. 2004; Karr et al. 2004). Although salvage logging has not been tested extensively, it is frequently justified as improving ecosystem function and recovery (Reeves et al. 2006).

Livestock grazing in riparian areas also has been shown to change composition and quantity of streamside vegetation, decrease discharge and increase summer water temperatures (Armour, Duff and Elmore 1994). Saunders and Fausch (2005) found grazing intensity and duration influenced the subsidy of terrestrial invertebrates to streams. While we know more about the effects of grazing on streams, we do not understand the effects of fire combined with grazing.

The majority of work on the effects of fire on macroinvertebrate communities has focused on benthic invertebrates, with little work on invertebrate drift or emergence following fire. By considering the latter, we can examine how fire influences movement of energy downstream and between freshwater and terrestrial systems. We expected fire effects as measured by movement of aquatic invertebrate density and biomass from headwater streams to adjacent systems to be different than recorded effects on benthic communities in other studies. By understanding fire effects on energy flow, we hope to develop insight into potential effects of fire on invertebrate consumers.

The patchy and unpredictable nature of wildfires makes a study design with watershed replication difficult. The spatial extent of the Togo fire allowed five replicate burned and five replicate control watersheds of similar size, logging history and area burned, which provided strong statistical power to test hypotheses and make comparisons to other studies. The objectives of this study were to compare 1) the in-stream response of

benthic invertebrate communities between burned and control watersheds and 2) the response of invertebrates leaving sites as drift and emergence from burned versus control watersheds. These objectives were accomplished by comparing direct measures of invertebrate density, biomass, community structure and composition.

Site Description:

This study took place in the Kettle Mountain Range of the Colville National Forest in northeastern Washington. The Kettle Mountain Range is the most easterly portion of the Cascade Range and western most of the Rocky Mountains, sharing characteristics of both ranges. The forest receives both maritime and continental weather systems; the east side of the Kettle Mountain Range receives 64-76 cm of precipitation annually and the west side 51-64 cm (Williams et al. 1995). The Togo Fire was a lightning-ignited fire, which burned 5000 acres in August – September 2003 (Fig. 1). It burned intensely through mixed conifer forest of western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*) and western red cedar (*Thuja Plicata*).

This study was conducted in 10 small 1st and 2nd order fishless headwater streams ranging in elevation from 1000 to 1500 m (Fig. 1). Sampling occurred in the summers of 2004 and 2005 and began 1-2 weeks after snowmelt, mid June in 2004 and late May in 2005. Study sites were located in tributaries of four streams; Independent (IND), Manley, Middle Fork Little Boulder (MFLB) and North Fork Lone Ranch (NFLR) Creeks. Burned sites were located within two tributaries of North Fork Lone Ranch, two tributaries of Independent and one tributary of Manley Creek; these subwatersheds

ranged in size between 0.14 and 0.87 km^2 and were entirely within the severe burn area. In this severe burn area, both canopy vegetation and understory plants and shrubs were completely burned to the stream. Control sites were located within three tributaries of Middle Fork Little Boulder Creek and two tributaries of Independent Creek; these subwatersheds ranged in size between 0.40 and 1.35 km^2 and were entirely outside of the burned area (Fig. 1). Fifty-meter reaches of each study stream were selected based on similarities among sites (Table 1). Sites that appeared to be perennial were selected although one control site (MFLB 1) dried completely late in the summer of both years and one burned site (IND 2) dried in July 2004. The burned site was moved upstream to where flow was perennial. The control site was not sampled the months it was dry but data from other months were used. No metrics calculated from this intermittent site were significantly different from other perennial control sites sampled.

Since 1995, management practices on the Colville National Forest have followed Inland Native Fish Strategy (INFISH) guidelines that require a minimum 45-m riparian buffer on perennial, fishless streams ("Inland Native Fish Strategy Environmental Assessment" 1995). Salvage logging occurred following the fire in 2003 and 2004 through much of the burned area, and this minimum 45-m riparian buffer was maintained at salvage logging sites. All sites were located in either mature live or burned forest and were selected to have at least a minimum 45-m buffer. Cattle grazing occurred throughout the study area. Cattle were brought onto the forest in June of both years and were fenced off from one burned site (NFLR 2) in 2005.

Methods

Sampling Methods:

Stream gradient, width, canopy cover, substrate, temperature, and grazing level were measured for each study reach. Gradient was measured with a handheld clinometer over the reach, and canopy cover was measured from the center of the stream at 1 m above the stream with a densiometer at four evenly spaced locations in each stream reach once each year after leafout. Temperature was recorded with TidBit® temperature loggers. Loggers were placed in streams in July 2004 and recorded temperature every hour through August 2005; only summer months were used in calculating mean and maximum temperatures. Stream width and depth measurements, and a visual estimate of dominant substrate were recorded for each sampling date and location. Mean width was calculated by taking an average of all widths recorded from each sample type and period at each site. At each site and sampling date, cattle grazing was classified by visual observations on a rating scale from 0 to 2 depending on grazing extent (Table 2).

Drift, emergence and benthic samples captured invertebrate export from streams to adjacent ecosystems and the invertebrate community within the streams. Drift was collected continuously for 48-hr once per month during the summers of 2004 and 2005 using methods from Wipfli and Gregovich (2002). A 10-cm PVC pipe approximately 1-m long was placed at the bottom of each reach with a 250-μm mesh net attached. Sandbags were placed in the stream to secure the pipes and to divert as much surface flow as possible through the pipe. When nets were set out and collected, discharge through each pipe was estimated by measuring the time required to fill a container of

known volume. Pipes were placed on the bottom of the stream bed and extended above the surface of the stream so invertebrates drifting at any point in the water column were captured. During high flows in May and June 2005, discharge at some sites exceeded pipe capacity. Because all ten sites could not be sampled concurrently, nets were placed at five sites one day and five the following day then collected the following two days to provide one day of overlap when nets were out at all sites. This minimized differences due to thunderstorms and short term increases in discharge.

Four randomly placed emergence traps were set in the stream at each site. Traps were 0.6-m long by 0.3-m wide by 0.5-m high wooden A-frames that covered 0.2 m^2 of stream bottom. No-see-um netting covered the traps and was held to the stream bottom with rocks and sticks. Plastic containers with approximately 5 cm of water and a drop of soap to break surface tension were set 20 cm down from the top of the netting. After 48-72 hr, all insects in the wells and insects flying inside the net were collected and preserved in 85% ethanol. During strong summer thunderstorms in August 2004, high flows disturbed traps at four of five burned sites and two of five control sites. This month was excluded from analysis.

A surber sampler with 500-μm netting was used to collect benthic invertebrates from five randomly selected locations in each reach. In 2004 a standard size sampler that collected from an area of 0.46 m^2 was used. Small stream size made it difficult to find a suitable location for this larger sampler, and in 2005, a smaller surber sampler with an area of 0.12 m^2 was used. Samples were collected from riffles whenever possible, but in some locations it was only possible to sample pools or very slowly flowing water.

Benthic samples were analyzed for four sampling periods (June and August of both years).

Algal samples were collected in each month of summer 2005 from six rocks randomly chosen from each site. Samples from an area of 0.09 cm^2 per rock were scrubbed, stored in the dark and frozen until analysis. Chlorophyll *a* was extracted from one half of each algal sample three weeks after collection using hot ethanol extraction as described in Sartory and Grobbelaar (1984). The other half was used to calculate algal dry mass (DM) and ash free dry mass (AFDM).

Sample Processing:

Invertebrate samples were preserved in the field with 85% ethanol. Replicate benthic and emergence samples from each site were combined into one composite sample for each site and sample type. Sub-sampling was required due to the large volume of invertebrates and detritus in drift and benthic samples. A minimum count of 300 individuals was enumerated and identified for each benthic and drift sample. Using either a Caton Tray or a Folsom Plankton Splitter samples were sub-sampled until the 300-individual mark was reached (Caton 1991; Carter and Resh 2001). Samples were sorted under a dissecting scope. Aquatic invertebrates were identified to family or genus level and terrestrial invertebrates to order. Invertebrates were measured to the nearest millimeter to determined biomass using length-weight regression equations (Meyer 1989; Burgherr and Meyer 1997; Sabo, Bastow and Power 2002). Identification keys and functional feeding group classification were used from Merritt and Cummins (1996).

Analysis:

Analyses of variance (ANOVA) using R version 2.1.1 were performed to test for differences in invertebrate biomass, density, community composition and community structure metrics for sites grouped by type. Site type (burn or control), month, year and an interaction between year and site type were the main factors ($\alpha < 0.05$). The interaction term determined if burned sites were more similar to control in 2005 than 2004. It was omitted when non-significant and analyses were rerun. Response variables of biomass and density were standardized by discharge and time or area sampled and log transformed to meet normality assumptions. Untransformed data were used for presentation purposes. Community composition was analyzed by testing differences in Shannon-Weiner diversity

$$H' = -\sum p_i \log p_i$$

where p_i is the proportion of individuals found in the *i*th taxa, Simpson's evenness

$$E_{1/D} = (1/D)/S$$

where D is the probability that any two individuals belong to the same taxa and S is taxa richness, % EPT density, and % Chironomidae density in burned compared to control sites. Evenness was calculated for all burned and control sites and sample dates combined, all other metrics were calculated for individual sites and sampling dates. Grazing effects were analyzed by an ANOVA testing for differences in log transformed invertebrate biomass and density among observed grazing levels for each sample type at burned sites (Table 3).

Non-Metric Multidimensional Scaling (NMS) on PC-ORD version 4 software was used to look at differences in community composition by density at sites along environmental gradients. Taxa that were present at < 5% of sites were grouped with the next higher level taxa (McCune and Grace 2002). Invertebrate abundance was standardized by discharge and time or area sampled and was square root transformed to normalize distributions. Bray-Curtis distance measures were used to calculate the distance matrix. Stress, which is a measure of the distortion in the arrangement of sites and increases with fewer dimensions, was considered acceptable when less than 20. Number of dimensions were determined by choosing the number beyond which there was little decrease in stress (McCune and Grace 2002). Linear correlations between taxa and axes were determined using Pearson's *r* values (See appendix A).

Results

Site Characteristics:

Stream discharge at burned sites ranged from 4.3 to 8.3 m^3 hr^{-1} and 2.8 to 15.2 m^3 hr^{-1} at control sites. Average summer water temperature at burned sites was 1.4°C warmer than at control sites, and mean maximum temperature was 5.3°C warmer at burned than control sites (Table 4). Canopy cover, including overstory canopy, live or burned trees and understory vegetation, at burned sites (average = 36%) was half that of control sites (average = 81%) (Table 4). There was no detectable difference in average canopy cover at burned sites from 2004 to 2005 ($p > 0.05$). Based on samples collected in 2005, there was no detectable difference in algal biomass or chlorophyll *a* between burned and control sites (biomass; $p > 0.05$, chlorophyll *a*; $p > 0.05$) (Table 4). Both AFDM and chlorophyll *a* were highly variable with AFDM at NFLR 1 two-fold higher than at any other site and chlorophyll *a* at MFLB 2 twice as high as all other sites. Chlorophyll *a* increased throughout the summer at both burned and control sites ($p = 0.03$).

Drift and Benthic:

Headwater streams in burned watersheds had significantly higher benthic densities of invertebrates (Fig. 2b) and exported significantly greater densities of invertebrates in drift (Fig 2a) than headwater streams in unburned watersheds (drift; $p < 0.001$, benthic; $p = 0.009$). Total flux of invertebrates in drift was also greater from burned sites averaging 85.6 individuals $stream^{-1}$ hr^{-1} at burned sites and 26.4 individuals $stream^{-1}$ hr^{-1} at control sites. Benthic and drift density varied by month and year with

higher density in 2004 than 2005 and generally greater densities late in the summer than early in the summer. Although invertebrate density was greater in burned sites, there was no significant difference in the biomass of invertebrates between streams from burned and unburned watersheds ($p > 0.05$) (Figs. 3a, 3b). Total flux of invertebrate biomass was similar between burned and control sites with a mean of 26.5 mg $stream^{-1}$ hr^{-1} at burned sites and 30.0 mg $stream^{-1}$ hr^{-1}. For both density and biomass, there was no significant interaction between year and site type. As burned sites in 2005 were not more similar to control sites than in 2004, no succession or recovery was detectable with these measures.

Average Shannon-Weiner diversity was consistently lower at burned than control sites (drift and benthic; $p < 0.001$) (Fig. 4a, 4b). Invertebrate community composition was dominated by Chironomidae in burned sites for both drift and benthic samples and percent Chironomidae was significantly greater in burned than control sites (drift and benthic; $p < 0.001$). Average percent chironomids over the entire study period comprised 56% of abundance in drift and 51% in benthic samples at burned sites, compared to 21% drift, 27% benthic at control sites (Fig. 5a, 5b). These differences were also represented in the evenness of community composition as measured by Simpson's Evenness. Drift samples were more even in community composition at control sites ($E_{(1/D)}= 0.112$) than at burned sites ($E_{(1/D)}= 0.017$). Similarly, in benthic samples evenness was 0.036 in burned sites and 0.085 at control sites. Percent Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa by density, was significantly lower at burned than control sites (drift; $p = 0.002$, benthic; $p = 0.005$). EPT in drift samples averaged 23% in burned sites and 40% in control sites (Fig. 6a) and 25% and 36% from burned and control sites in benthic samples

(Fig. 6b). Succession in burned sites from 2004 to 2005 was not statistically detectable. Taxa richness was highest in drift samples, generally higher at control sites and was variable between 2004 and 2005 (Table 5). The decrease in taxa richness in the benthic samples between 2004 and 2005 was likely due to the use of the smaller surber sampler used in 2005.

Invertebrate community composition in drift was dominated by Diptera (64%) at burned sites with increases in Ephemeroptera in August of 2004 and 2005 (Fig. 7a). Percent terrestrial invertebrates in drift samples was highly variable, ranging from 1-50% of total invertebrate abundance and there was no significant difference in percent terrestrial invertebrates between burned and control sites ($p > 0.05$). In benthic samples, community composition was more similar between burn and control sites, though Plecoptera increased in burned sites in August of both years (Fig. 7b). Collectors (both filterers and gatherers) dominated at both burned and control sites, but there were significantly greater proportions of collectors at burned than control sites (benthic and drift, $p < 0.001$) (Fig 8a and b).

A three dimensional solution ($r^2 = 0.83$, stress = 13.7) to a NMS analysis of 59 drift samples resulted in a clear separation between burned and control sites along the 1st axis (Fig. 9a). Chironomidae, *Baetis* and Simuliidae had the strongest gradient along the first axis with greater abundances at burned than control sites (Appendix A). These taxa contributed to the higher proportion of collectors at burned sites noted previously. Samples taken in 2004 separated from those taken in 2005 along the 3rd axis (Fig. 9b). There were large environmental differences between 2004 and 2005 with warmer water

temperature (12.1°C) and lower discharge (5.6 m^3 hr^{-1}) in 2004 than 2005 (10.6°C and 9.3 m^3 hr^{-1}) that likely contributed to differences between sample years. Flatworms (Turbellaria) and terrestrial invertebrates, primarily Hymenoptera, were more abundant at burned and control sites in 2004, while *Chyranda* (Limnephilidae) was more abundant at control sites in May and June of 2005. The 2nd axis was negatively correlated with month sampled with greater abundances of *Dixa* (Dixidae) and *Yoraperla* (Peltoperlidae) at the end of the summer.

NMS ordination of 38 benthic samples resulted in a three dimensional solution (r^2 = 0.91, stress = 10.0) that showed a grouping of burned sites from June of both years, a grouping of control sites from June and a grouping of burned and control sites from August of 2004 and 2005. There is less clear separation of burned and control sites in the samples taken in August (Fig. 10). Sites were separated along the 1st and 3rd axes by a gradient of water temperature, discharge and month (June or August) sampled. The scrapers *Cinygmula* (Limnephilidae) and *Chyranda* were positively correlated with the 3rd axis (Appendix B). While neither of these taxa were highly abundant at any site, they were only present at control sites in June of both years with rare exceptions. Chironomidae, *Lepidostoma* (Lepidostomatidae) and *Baetis* were negatively correlated with the 3rd axis and more abundant at burned sites. Heptageniidae, Chloroperlidae, Perlodidae and Hydracaria were negatively correlated with the 1st axis and more abundant at both burned and control sites in August of both years than in June. There was also some separation between burned and control sites along the 2nd axis. Chironomidae, *Baetis* and Simuliidae, the latter being collector-gatherers, were strongly correlated with

this axis and more abundant at burned sites. Unlike drift samples, there was no clear separation among benthic assemblages by year.

Emergence:

Compared to drift and benthic invertebrates, invertebrate adult emergence showed more consistent difference between burned and control sites. Over the entire sampling period, both density and biomass of adult emergence were significantly greater in burned than control sites (density, $p = 0.004$; biomass, $p = 0.03$) (Fig. 11a). In 2004, biomass and density from burned sites were much greater than from control sites, while in 2005 there was little to no difference resulting in a significant interaction between treatment and year (density, $p = 0.012$; biomass, $p = 0.04$) (Fig. 11b). For both density and biomass, there was significantly less emergence early than late in the summer.

For 2004 and 2005 samples combined, Shannon-Weiner diversity of emerging invertebrates was lower at burned sites than control sites ($p < 0.001$) (Fig. 12), with a significant interaction between site type and year sampled ($p = 0.001$). When samples from 2004 and 2005 were analyzed separately, there was no significant difference in emergence from burned sites in 2005. Community composition of emerging invertebrates showed a different pattern than composition in benthic and drift samples. There was no significant difference in % EPT taxa emerging from burned and control sites ($p > 0.05$) (Fig. 13a), primarily due to a large increase in EPT emerging from burned sites in June 2005. Significantly more chironomids emerged from burned than control sites ($p < 0.001$) (Fig 13b). The difference between percent chironomids in burned and control sites was less in 2005 than 2004, accounting for a significant interaction ($p = 0.003$) between site

type and year sampled. Taxa evenness ($E_{1/D}$) from emergent samples was 0.046 from burned sites and 0.087 from control sites. Taxa richness in emergence was lower than for other sample types. Richness was greater in 2005 than 2004 and unlike other sample types, was greater at burned than control sites in 2005 (Table 5).

As in the ordination of drift and benthic samples, site type and year sampled were separated in NMS ordination of 55 emergence samples; however, fewer emergent taxa were associated with the gradients identified. The ordination resulted in a three dimensional solution ($r^2 = 0.81$, stress = 15.3). Burned and control sites separated along the 2nd axis with a greater abundances of Chironomidae, Baetidae and other dipterans emerging from burned sites (Fig 14a). Sites sampled in 2004 separated from 2005 along the 3rd axis again with higher water temperature and lower discharge in 2004 than 2005 and greater chironomid emergence in 2004 than 2005 (Fig. 14b). The 1st axis was not highly correlated with any taxa or environmental variables (Appendix C) but had an r^2 of 0.23. As with the ordination on drift samples, variability in water temperature and discharge was highly correlated with year sampled but not correlated with sample type.

Cattle Grazing:

Cattle grazing at burned sites appeared to be more prominent at burned than control sites (Table 3) as it was easier for cattle to access the stream through the burned and recovering vegetation than through dense understory vegetation at control sites. The impact of cattle grazing was only analyzed at burned sites as there was a range of grazing levels. There were no detectable effects of cattle grazing on invertebrate density or

biomass from drift or benthic samples (Fig 15a and b). There were trends of greater density and biomass at sites with higher levels of grazing in the drift samples (Fig 15a).

Discussion

In the two years following forest fire, headwater streams from burned watersheds exported four times more invertebrates in drift, twice as many in emergence, and contained 2.5 times more invertebrates in the benthos than unburned sites. Increased density following increased light levels and subsequent higher primary production was predicted by Minshall (1989). Even with this increase in invertebrate density, there was no difference in the biomass of drifting or benthic invertebrates following fire; however, biomass of emerging aquatic invertebrates was greater in burned sites. Similarly, other studies found mixed and usually non-significant responses in invertebrate density and biomass in the first years following fire (Minshall et al. 1995; Minshall et al. 1997; Minshall, Royer and Robinson 2001a; Minshall et al. 2001b; Minshall 2003), except for Rinne (1996) who found significant decreases in invertebrate density following fire and flooding.

Community composition differed by sample type with an increase in *Baetis* at burned sites in drift but not in the benthos in August of both years (Fig. 7). Similar to findings from other disturbance studies (Anderson 1992; Minshall 2003), chironomids increased in all sample types in the two years following fire. Chironomids and *Baetis*, both early colonizing taxa with short life cycles and high reproductive rates, are frequently more abundant following fire and other disturbances (Anderson 1992; Minshall 2003). The increase in density and dominance of chironomids in burned sites is likely responsible for the decrease in diversity. Colonization was most likely from in-stream or hyporheic survivors or aerial dispersal by adults. Drift from undisturbed

upstream sources may typically be a source of colonizing invertebrates, but likely is not an important factor in this study as upstream reaches were as severely burned as the locations studied. An increase in these quickly reproducing taxa could result in the increased density in burned sites. These taxa, especially when collected early in their life cycle, are smaller than some longer lived taxa, such as many other EPTs, which were more abundant in control than burned sites, and may account for the lack of difference in invertebrate biomass.

There were very few predators, scrapers or shredders at burned sites. Collectors were dominant at all sites, particularly at burned sites. Although scraper and shredder densities were low, they were important in detecting differences in community composition. The scraper *Cinygmula* and shredder *Chyranda* were taxa that were highly correlated with control sites in June benthic samples. The predators Chloroperlidae and Perlodidae show in the benthic NMS as being highly correlated with both burn and control sites in August of both years. These taxa are more tolerant of warmer water and lower discharges that occurred late in the summer.

If algal growth increased, more scrapers, who graze periphytic and epiphytic algae off rocky and organic substrates, would have been expected (Minshall 2003). However, we did not observe increased algal growth following fire as either AFDM or chlorophyll *a*. Lack of algal growth following fire is contrary to initial predictions by Minshall (1989) but later studies also recorded no increase or decreases in primary production (Minshall et al. 1995). These patterns may be due to increased consumption and turnover at burned sites, but there was neither biological nor physical evidence to

support this explanation. Appropriate functional feeding groups were not present, and decreased bed stability with increased fine sediments suggested disturbance levels influenced algal abundance. Shading from rapidly recovering riparian vegetation in 2005 (primarily fireweed *(Epilobium augustifolium)*) may have contributed to similar rates of algal growth in burned sites compared to control sites.

There was no succession detected in drift or benthic samples from 2004 to 2005, although there were changes in community composition such as increased proportion of EPT and shredders from 2004 to 2005. An interesting difference between sources of invertebrates was that emergence from burned sites in 2005 was more similar to control sites than in 2004. Moreover, there were significant interactions between site type and year sampled in emergent biomass, density, % chironomid, % EPT and diversity. These differences may have been a sign of succession detectable in emerging invertebrate communities at the burned sites. Post-fire succession in aquatic ecosystems is expected to follow recovery of riparian vegetation and should be more rapid in headwater streams than larger rivers (Bisson et al. 2003). In 2005 there was riparian vegetation recovery and regrowth after the Togo fire which provided increased shading and may have contributed to succession in the aquatic community. High environmental variability between years was the consequence of a late season snowfall resulting in higher discharges and lower water temperatures in 2005 compared to 2004. These differences in temperature and discharge may have had a greater influence on the aquatic community than any vegetation recovery.

Different results from different sample types show the importance of measuring the aquatic community in multiple ways. The stronger, more consistent responses of emerging invertebrates to burned conditions provided an important tool for observing potential succession and delivery of invertebrates to the terrestrial environment. The stronger response in emergence may be due to overall lower numbers and less variability in number of individuals and taxa collected in emergence samples making differences easier to detect (Table 5). The response in emergence biomass likely reflects less difference in adult insect biomass compared to biomass of larvae that can range widely between early to late instars. Emergence samples also have an advantage in requiring less processing time than benthic or drift samples as invertebrates do not have to be sorted from detritus and adults can often be identified at a finer taxonomic scale than larvae.

Higher invertebrate densities mean more potential food to downstream and riparian consumers, and may provide an important pulse of food and subsidy to consumers following disturbance. The lack of increased drifting invertebrate biomass implies these individuals were on average smaller than those at control sites. More time and energy must be spent by drift feeding fish and other consumers to detect and capture smaller prey (Stephens and Krebs 1986). This study could not determine whether the increased numbers of small individuals in the drift would compensate for lower biomass consumption by drift-feeding consumers. With the increase in density as well as biomass in invertebrate emergence, there is an increase in food available and exchange to riparian consumers. This could be an important food supply to wildlife recovering from fire.

The fire regime and forest type of the Togo fire was similar to that of Yellowstone and fires in Idaho studied by Minshall et al. (1989; 2001a), but they differ in management history. It has been predicted that recovery from fire will be slower in areas with previous and post-fire anthropogenic disturbances (Bisson et al. 2003; Minshall 2003; Beschta et al. 2004; Karr et al. 2004; Reeves et al. 2006). In this ecosystem there has been a history of anthropogenic disturbances such as cattle grazing and logging. One of the few fire studies in an area with previous management activities found more severe responses to fire with decreases in invertebrate and fish densities to almost zero following fire and flood (Rinne 1996). Post-fire flooding similar to that described by Rinne (1996) occurred at one burned site in August 2004 following heavy thunderstorms. While this flood scoured and reorganized the channel, invertebrate density from benthic samples taken three days after this event, was slightly higher than in June 2004 but much lower than benthic densities in 2005. Rinne's study occurred in the southwestern US in a ponderosa pine forest with a very different fire regime than in these other regions. Responses to the Togo fire would be expected to be and are more similar to findings from the studies in Yellowstone and Idaho with differences potentially due to differences in management activities. At sites with higher levels of cattle grazing, tendencies toward higher invertebrate densities and greater chironomid abundance were detected, but these were not significant. There was also no pattern in percent terrestrial invertebrates in drift with grazing level as found by Saunders and Fausch (2005), although grazing levels and terrestrial invertebrate sampling methods were different in these studies. It may be that there was no additional effect of grazing at burned sites, or the coarse classification of

observed grazing levels could not capture the impact of cattle grazing, or the small sample size and low statistical power may have been insufficient to detect differences.

Maintaining riparian buffers may play an important role in both protecting these small streams and providing instream habitat. Salvage logging occurred at all of the burned sites but a 45-m riparian buffer was maintained. The additional influence of salvage logging could not be tested with this study design, but it is likely that retaining a buffer zone aided in recovery of riparian vegetation and therefore the aquatic system. The remaining burned trees provided some shade which helped moderate stream temperatures. There was likely less sedimentation and disturbance to the stream banks with this buffer which aided in regrowth of riparian vegetation. While this study did not directly test the effects of post-fire disturbance on aquatic communities, it suggests the need to compare response to fire in sites managed for either grazing or riparian logging.

Previous studies have shown a wide range of invertebrate responses in the first years following fire; from changes in community composition, but little change in density and biomass, to nearly complete loss of the invertebrate community (Minshall 2003). Responses vary by fire severity and forest type, but are also based on levels of anthropogenic disturbance. Unlike results following fire in undisturbed areas, there was a highly significant increase in invertebrate density but lack of difference in biomass; these results were not outside the range of variation of previous findings, and changes in community composition are very similar to other post-fire studies. Response was not as severe as that in a Ponderosa Pine ecosystem with anthropogenic disturbance. It is difficult to determine whether invertebrate response in the Togo Fire was influenced

more by fire severity and forest type or by other disturbances. Further studies directly testing the influence of previous and post-fire disturbances on aquatic ecosystems is necessary to make informed management decisions in preparing for and recovering from fire.

Conclusions and Management Implications:

The most important implications of this study may relate to consequences for downstream and terrestrial foodwebs in fire prone regions of the Pacific Northwest. Following intense wildfire, drift and emergence of invertebrates increased, thus increasing potential food availability for fish and other consumers, including those inhabiting riparian forests. If consumers are food-limited, then fire will likely affect consumers through this aquatic food source. In this case for example, more food may mean greater fish production or greater abundance of birds in riparian areas. It is uncertain what effect fire may have on these food resources beyond the two years examined in this study. Understanding longer-term effects, such as five or more years post-fire, would provide insight into the successional trajectories these foodwebs and ecosystems are likely to take following fire. Longer-term fire effects may be much different than the short-term effects recorded here, and less intense fires may have different effects as well. Wildfires are natural phenomena of these forests, helping shape their ecosystems (Bisson et al. 2003), including associated invertebrate communities. Management of fires and riparian forests will clearly affect fish and other consumers by affecting resource flow in these foodwebs.

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Figures

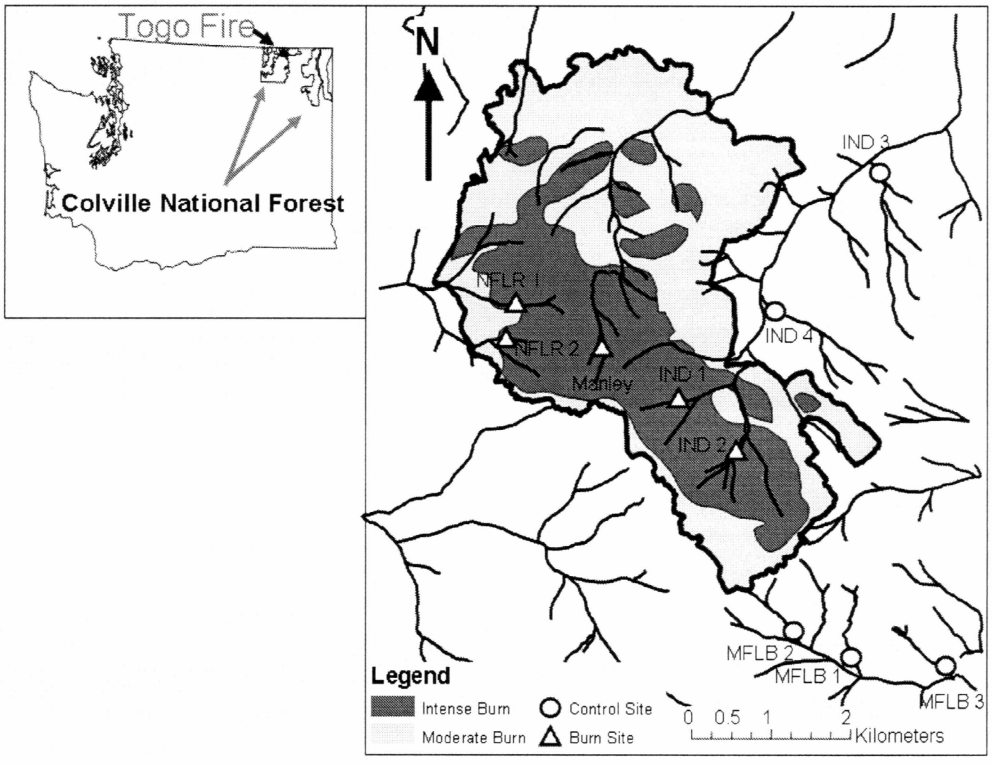

Figure 1. Location of the Togo Fire within the Colville National Forest in Washington. Fire boundary, area of intense burn and location of study sites in the Togo Fire area. IND (Independent Creek), NFLR (North Fork Lone Ranch Creek), MFLB (Middle Fork Little Boulder Creek), Manley (Manley Creek).

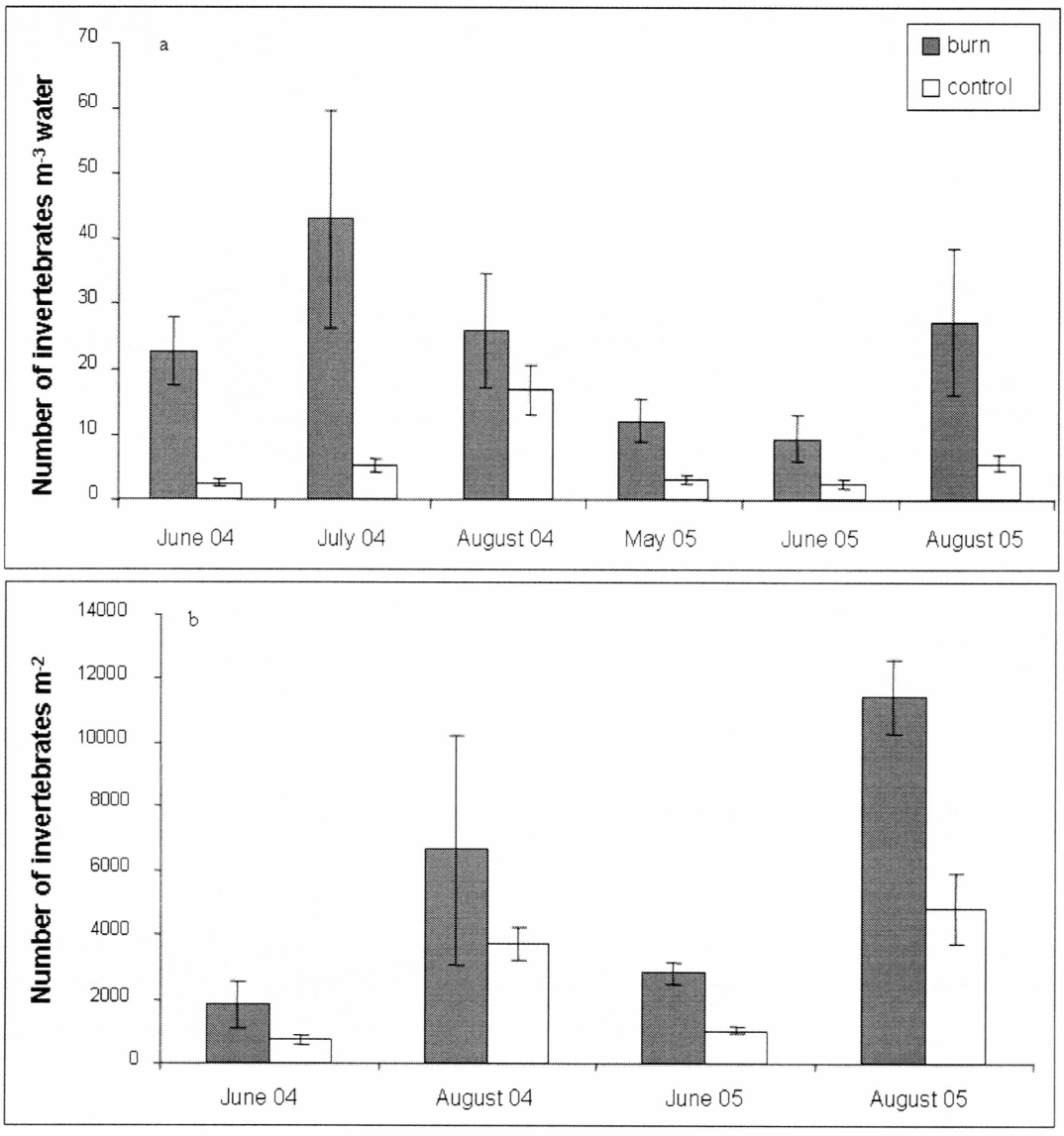

Figure 2. Mean invertebrate density in drift (a) and benthic (b) samples from burned and unburned (control) sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

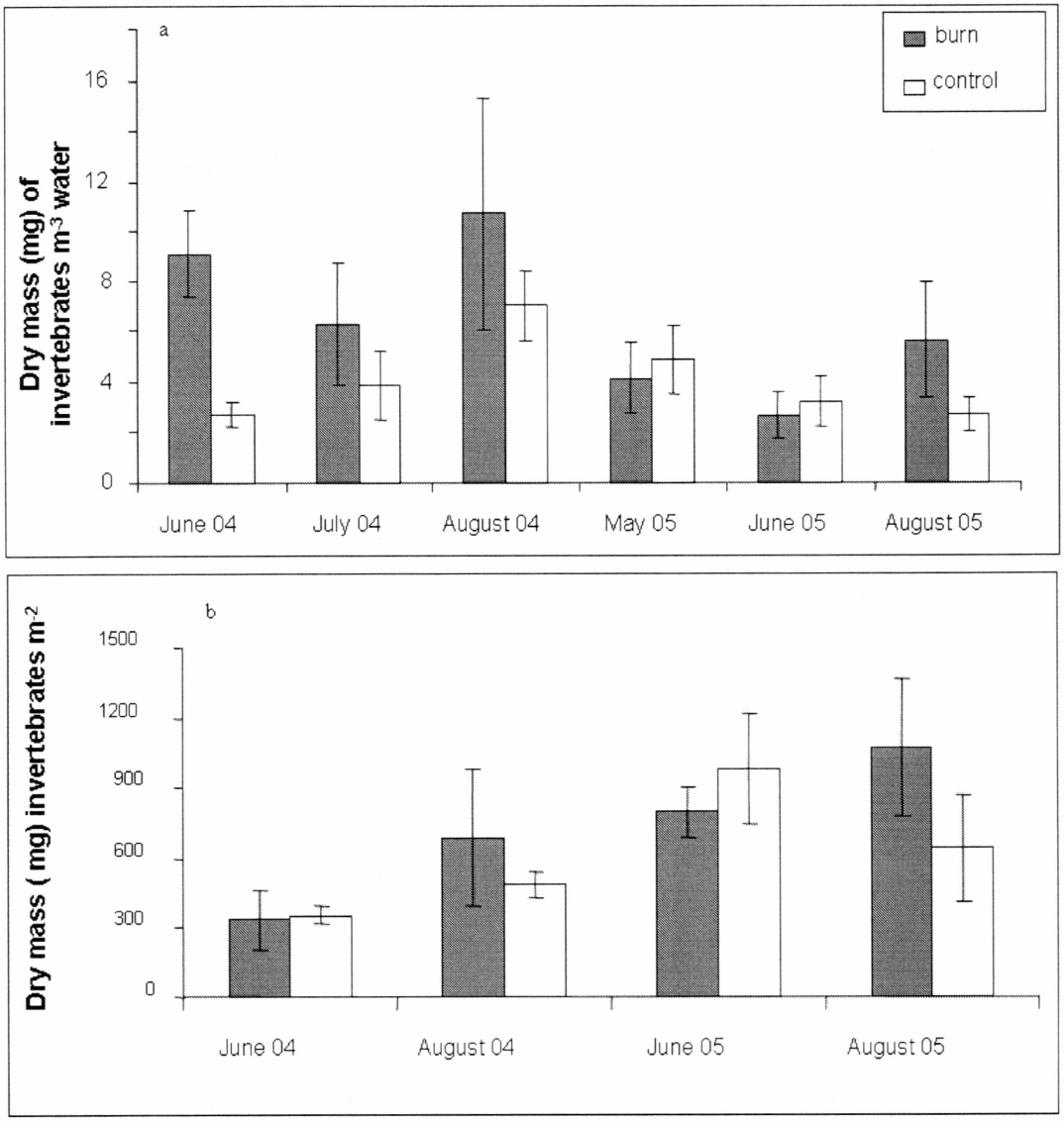

Figure 3. Mean invertebrate biomass in drift (a) and benthic (b) samples. Each bar represents the mean with standard error of five replicate streams in each sampling period.

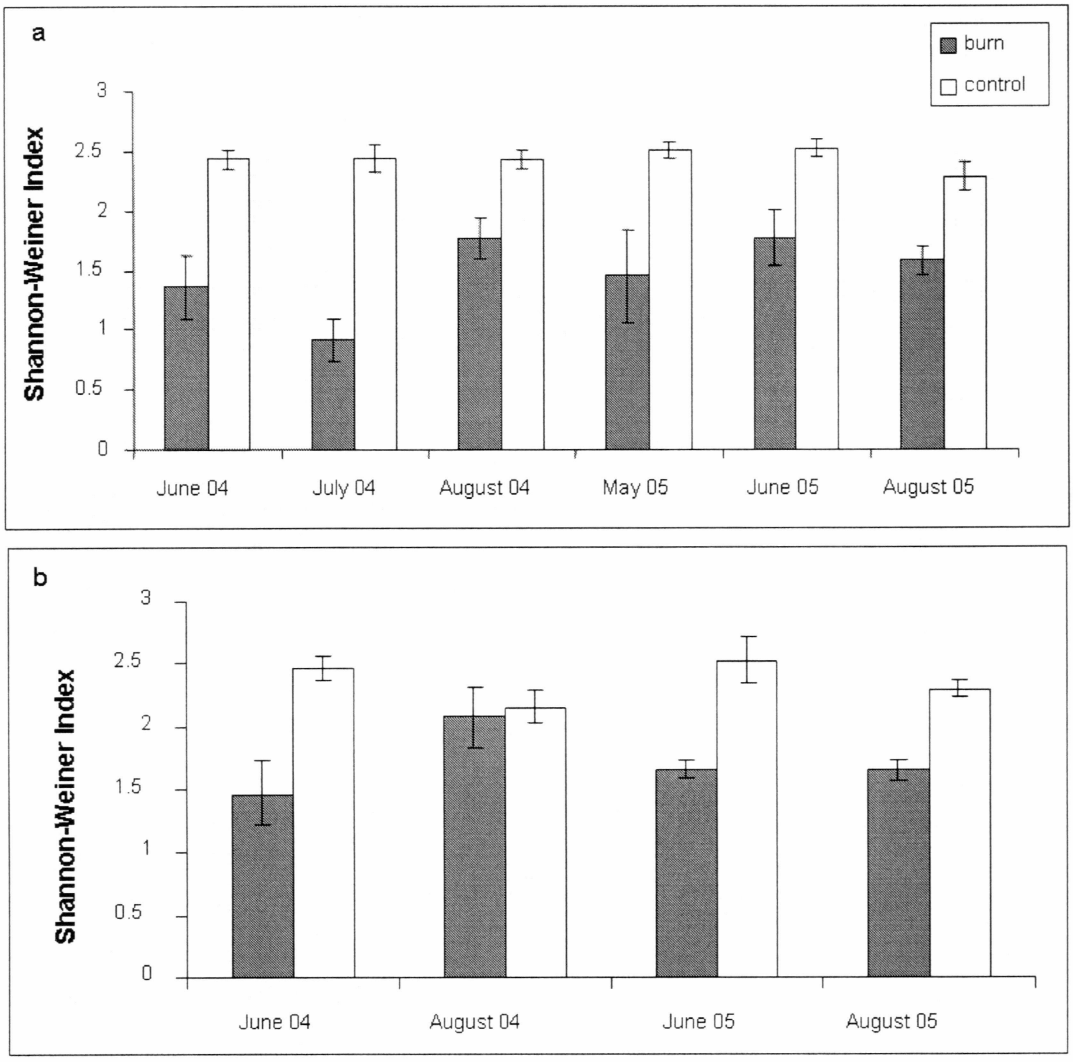

Figure 4. Mean Shannon-Weiner diversity of drift (a) and benthic (b) samples from burned and control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

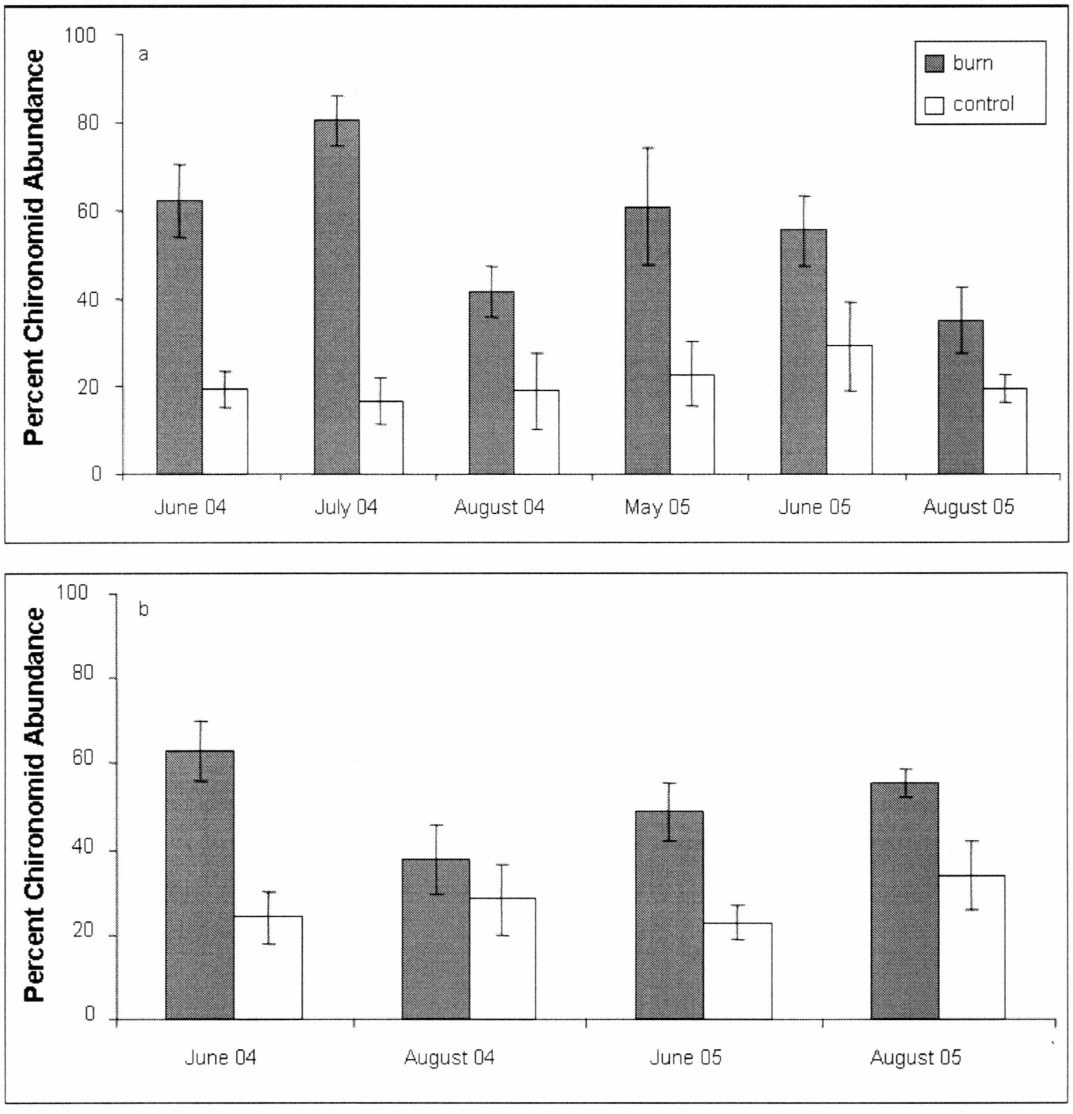

Figure 5. Mean percent by abundance of chironomids in drift (a) and benthic (b) invertebrate samples from burned and control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

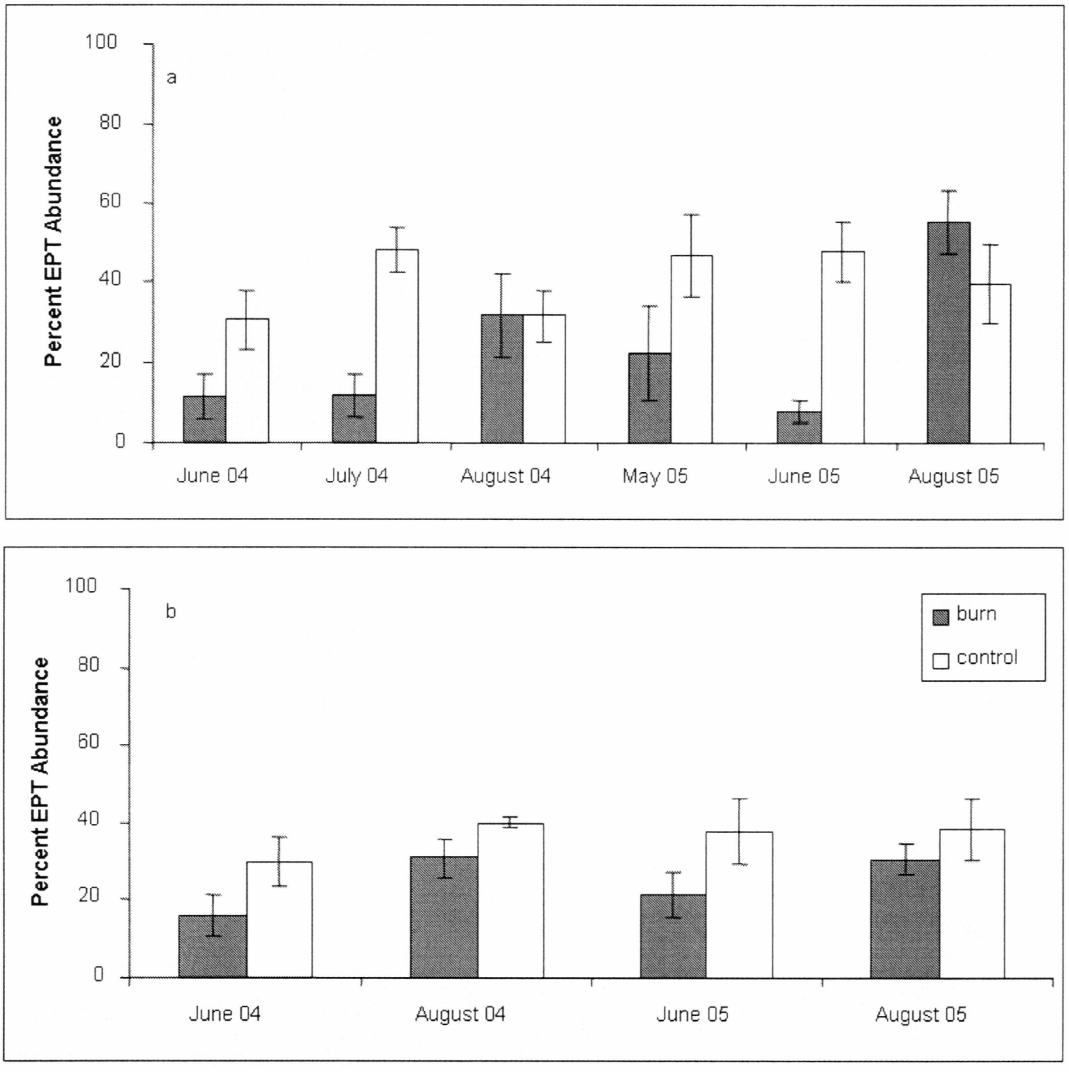

Figure 6. Mean percent by abundance of Ephemeroptera, Plecoptera and Trichoptera (EPT) in drift (a) and benthic (b) invertebrate samples from burned and control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

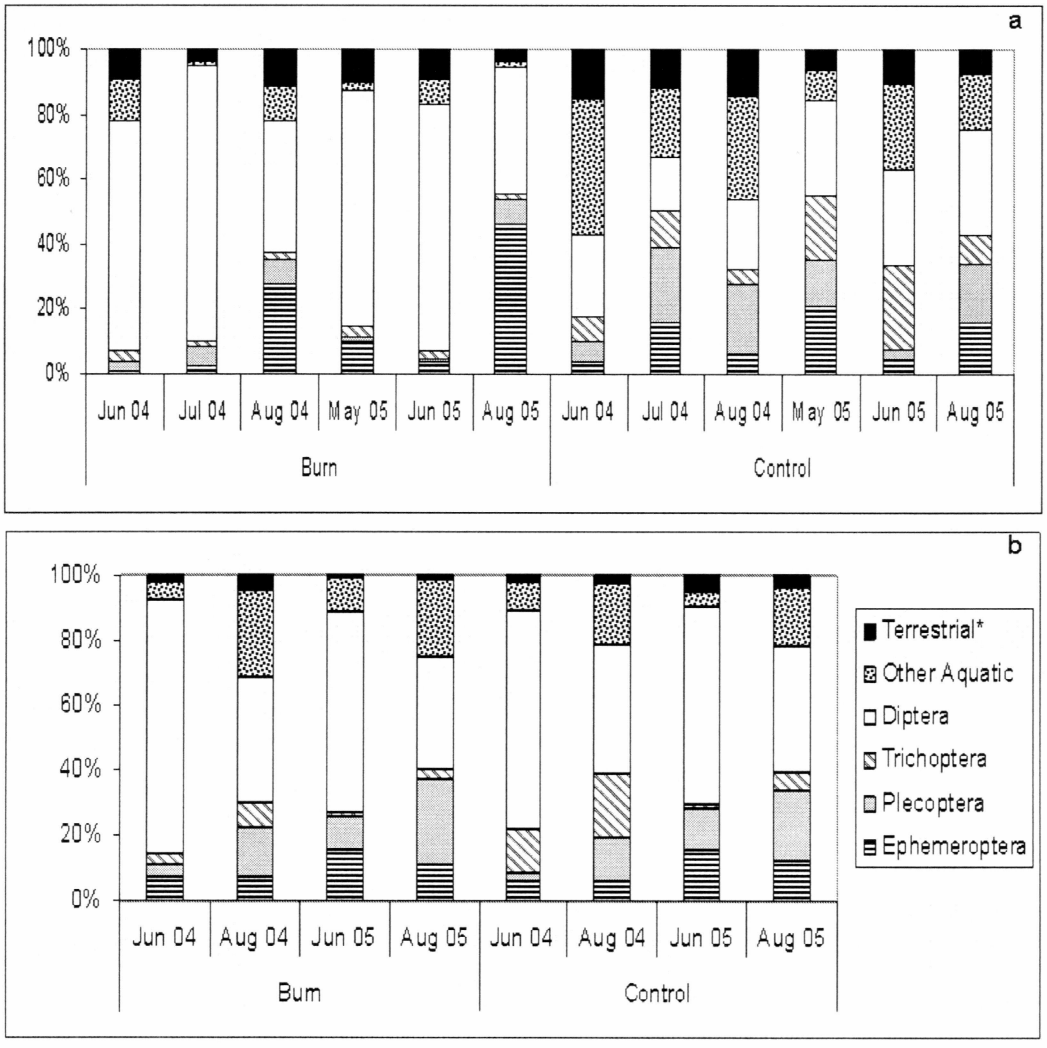

Figure 7. Community composition of drift (a) and benthic (b) samples.
*Terrestrial Invertebrates include adult stages of aquatic larvae.
Other aquatic includes primarily: Ostracoda, Copepoda, Gordiodia, Oligochaeta, and Hydracaria.

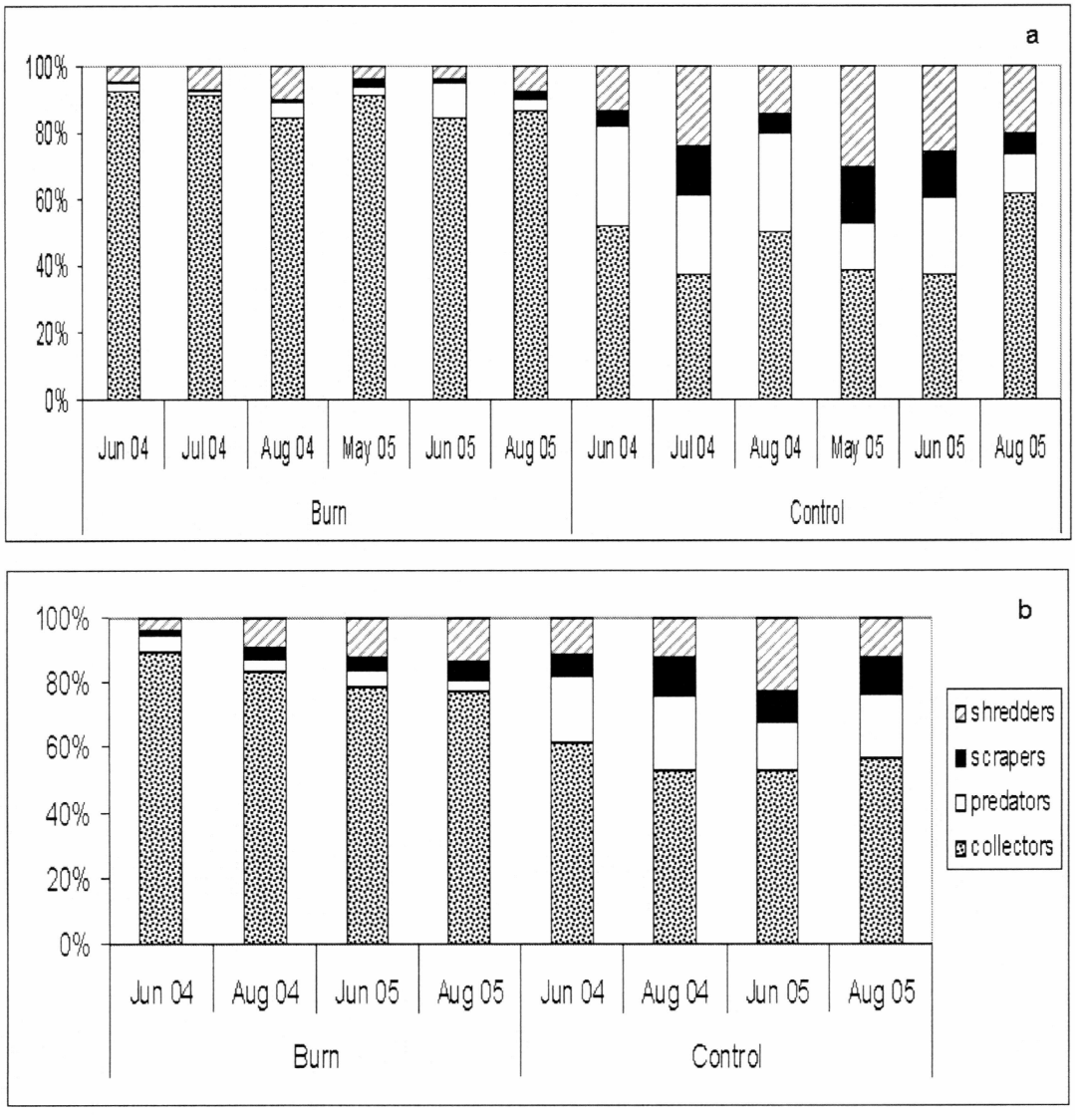

Figure 8. Functional feeding groups of aquatic invertebrates in drift (a) and benthic (b) samples.

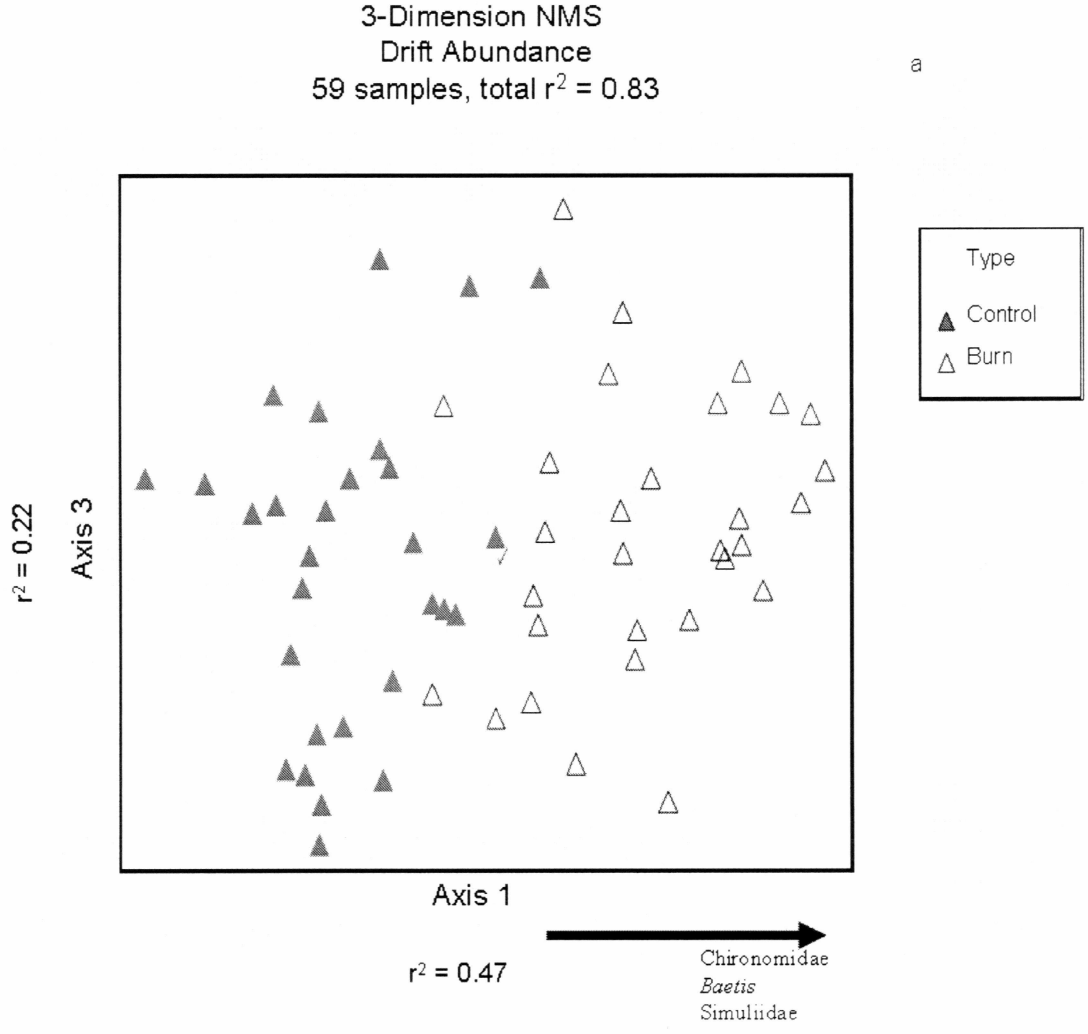

Figure 9. Three dimensional Non-metric Multidimensional Scaling ordination of invertebrate abundance in drift. Each point represents one drift sample from one site and one sample period. Axis 1 (a) represents a gradient between burned and control sites. Axis 3 (b) represents a gradient of in year sampled from water temperature and discharge.

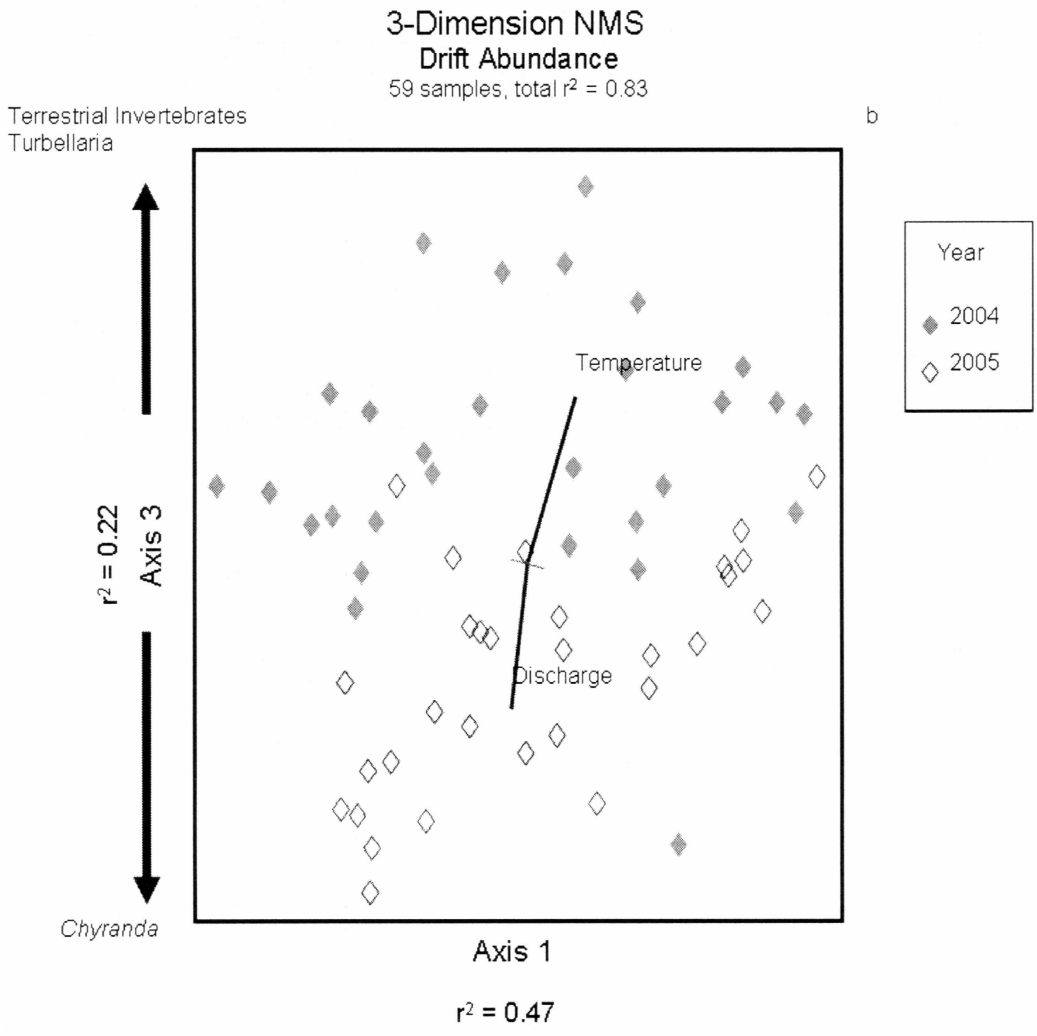

Figure 9 continued.

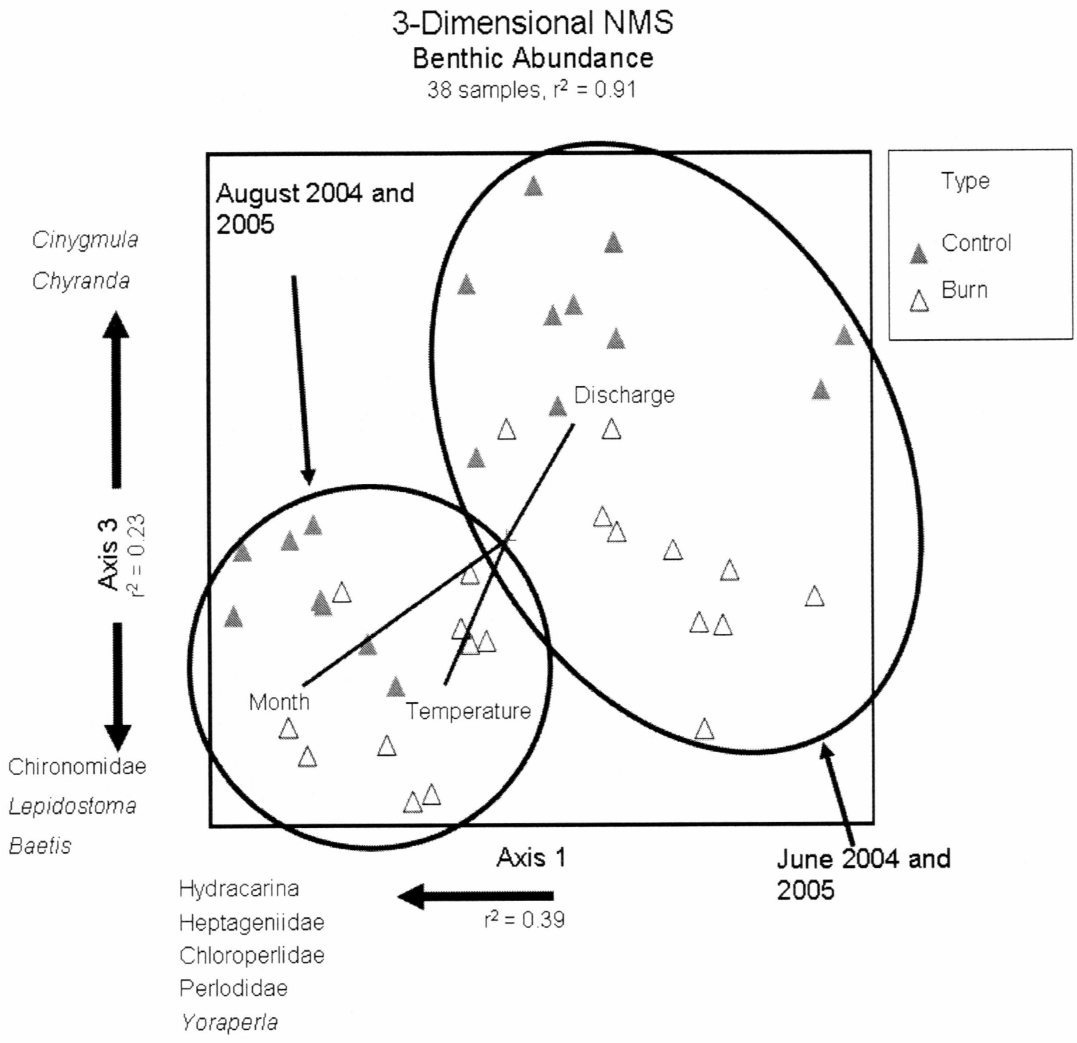

Figure 10. Three dimensional Non-metric Multidimensional Scaling ordination of invertebrate abundance in benthos. Each point represents one complied benthic sample from one site and one sample period. Circles enclose samples taken in August and June.

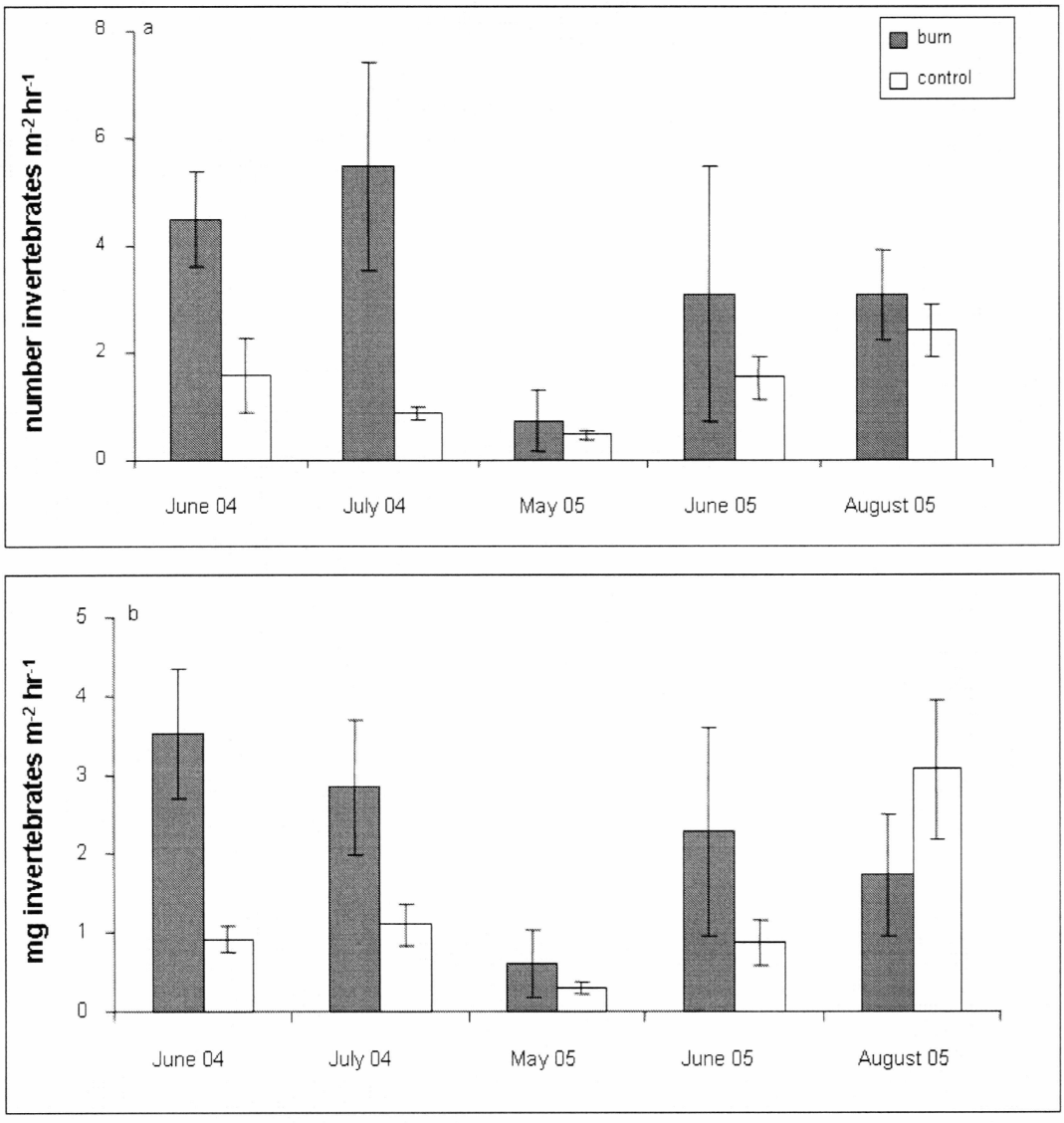

Figure 11. Mean invertebrate density (a) and biomass (b) from emergence samples at burned and unburned control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

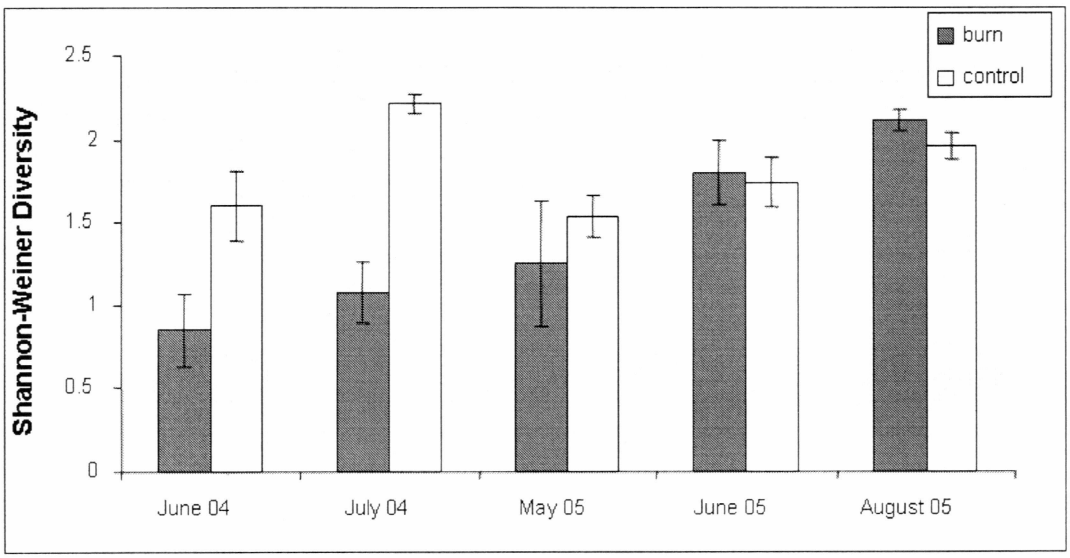

Figure 12. Mean Shannon-Weiner diversity of emergence samples from burned and unburned control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

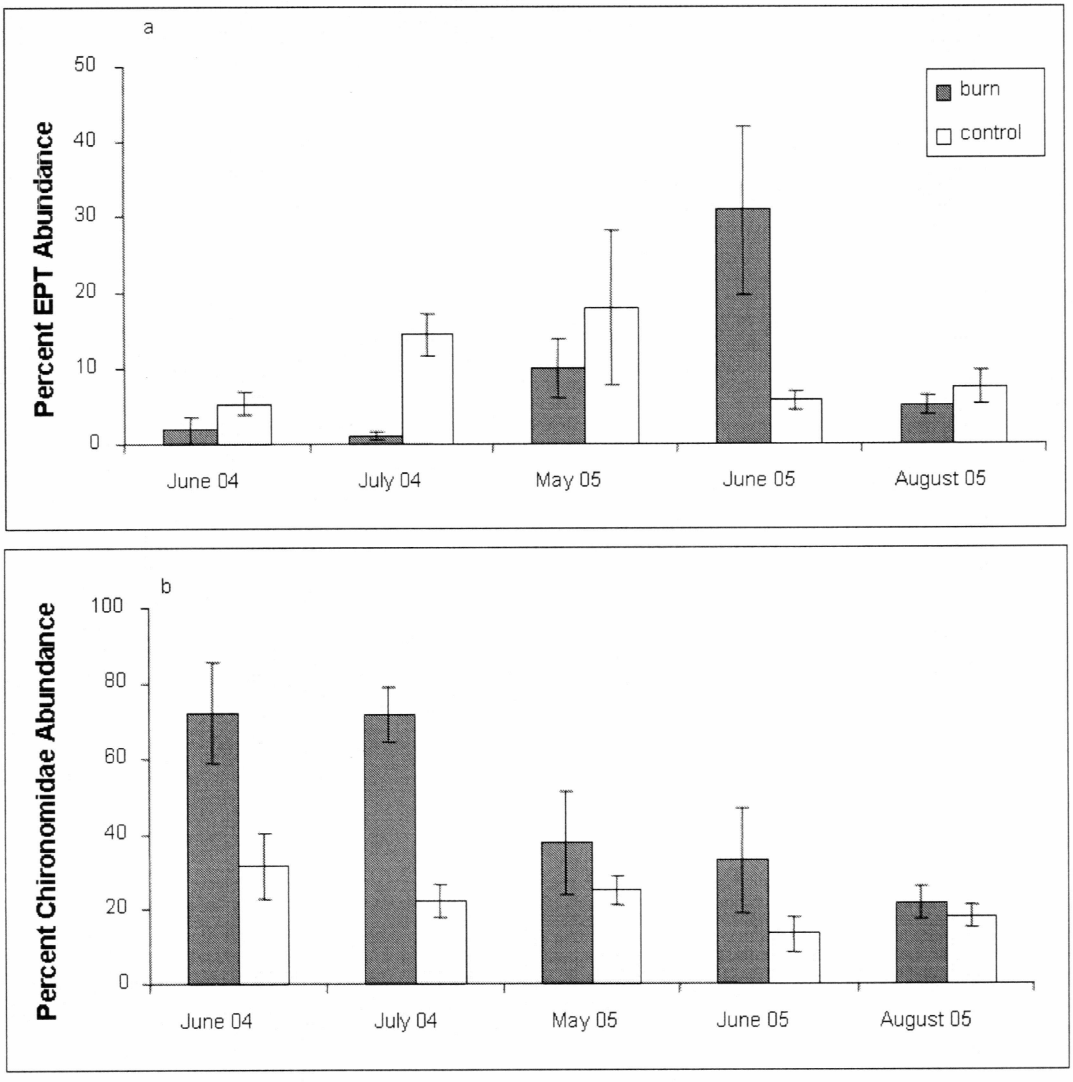

Figure 13. Mean percent by abundance of Ephemeroptera, Plecoptera and Trichoptera (EPT) (a) and Chironomidae (b) from emergence samples from burned and control sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

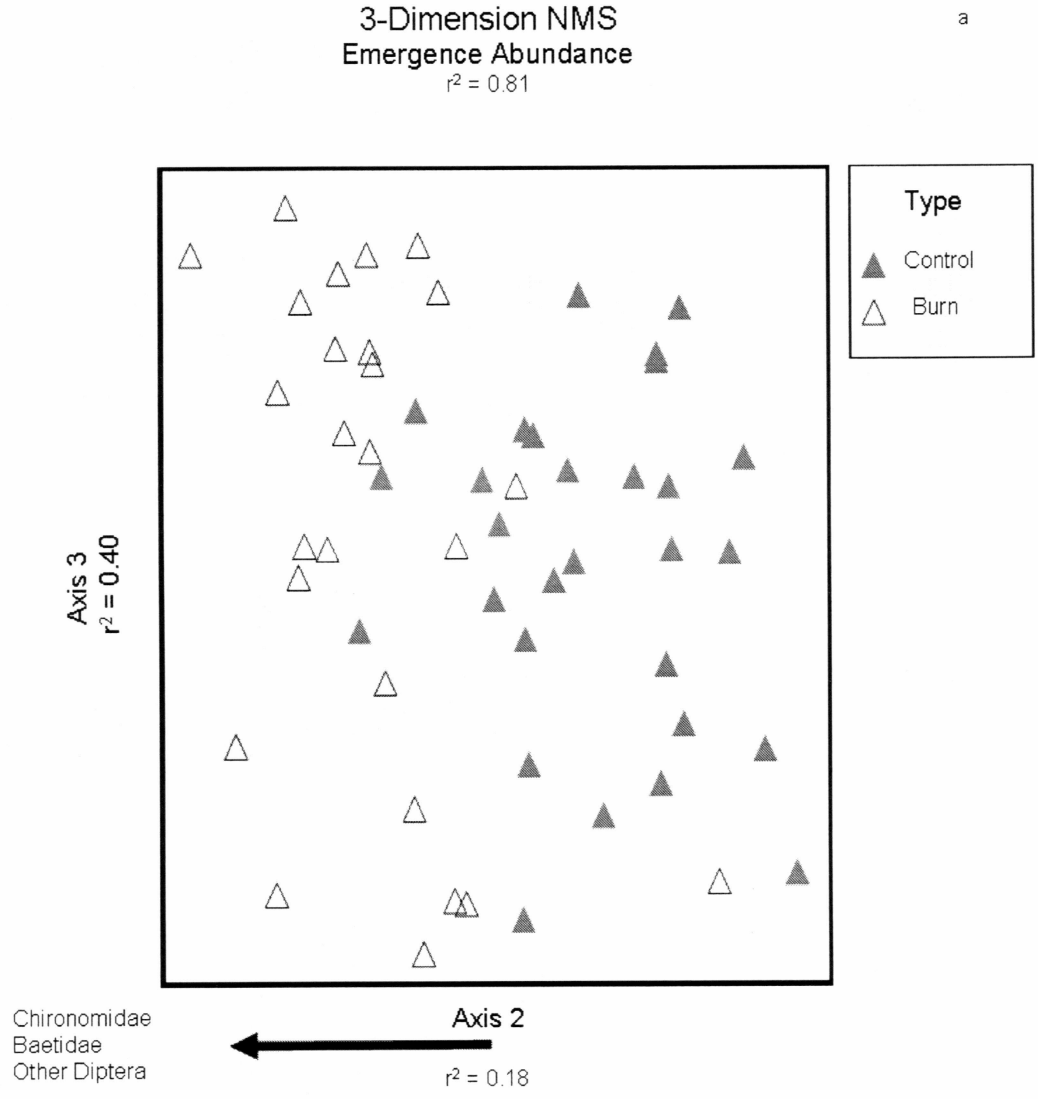

Figure 14. Three dimensional Non-metric Multidimensional Scaling ordination of invertebrate abundance in emergence. Each point represents one emergence sample from one site and one sample period. Axis 2 (a) represents a gradient between burned and control sites. Axis 3 (b) represents a gradient of in year sampled from water temperature and discharge.

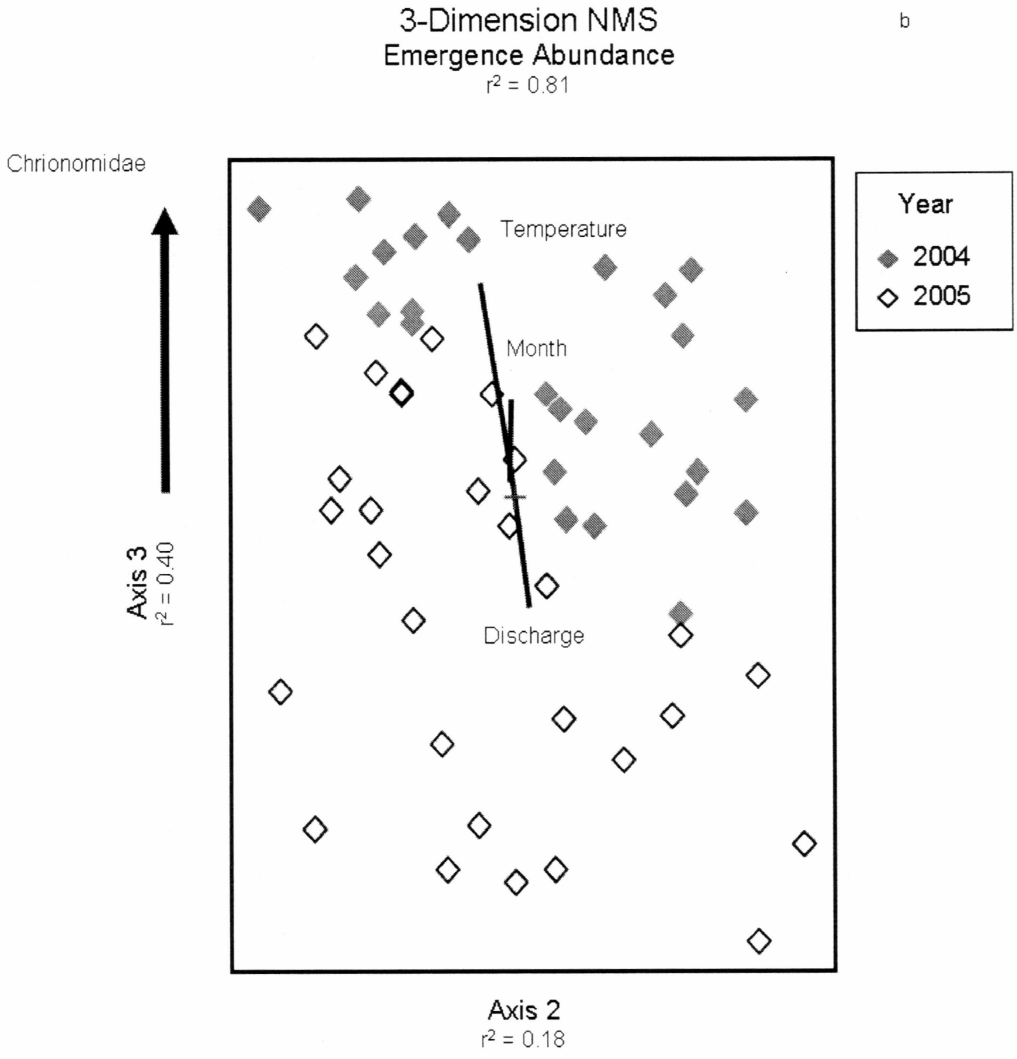

Figure 14 continued.

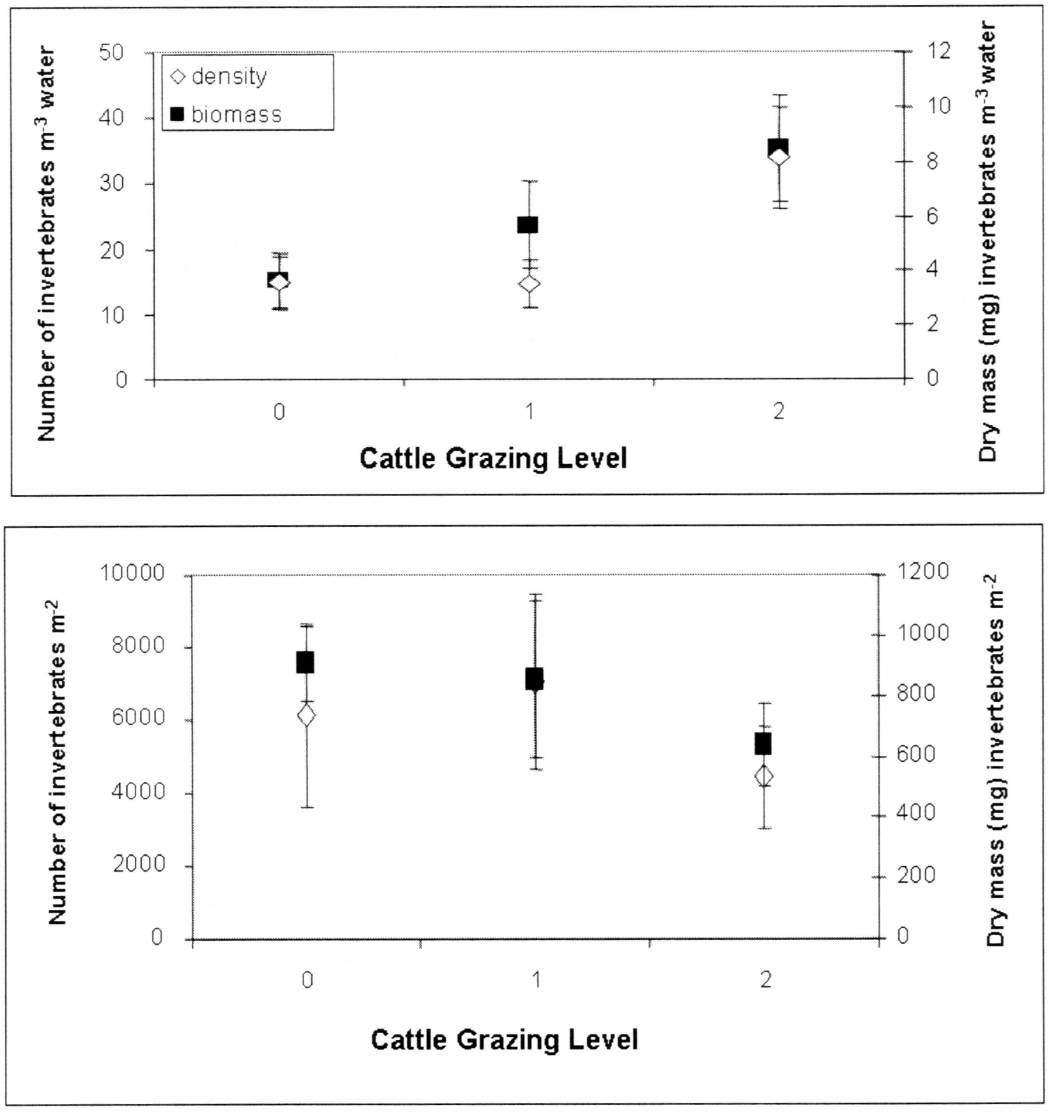

Figure 15. Invertebrate density and biomass by grazing level from drift (a) and benthic (b) samples of burned sites. Points represent the mean with standard error of burned streams with different levels of cattle grazing (0 = none, 1 = moderate, 2 = heavy).

Tables

Table 1. Watershed characteristics of Togo Fire study sites.

SITE	TYPE	ELEVATION (m)	WATERSHED AREA (km^2)	SLOPE	DRAINAGE ASPECT
IND 1	Burn	1450	0.24	11	N
IND 2*	Burn	1400	0.87	4	E
Manley	Burn	1410	0.14	6	N
NFLR 1	Burn	1310	0.32	22	W
NFLR 2	Burn	1290	0.37	13	W
IND 3	Control	1020	1.23	9	N
IND 4	Control	1210	1.35	8	NW
MFLB 1**	Control	1390	0.52	13	S
MFLB 2	Control	1460	0.40	11	SE
MFLB 3	Control	1290	0.44	9	SE
MEAN	Burn	1370	0.39	11	
	Control	1280	0.79	10	

* Site dried July 2004, sampling location moved upstream to site with continuous flow.
** Site dried August 2005.

Table 2. Classification system for observed level of cattle grazing.

CATTLE GRAZING LEVEL	0	1	2
Severity	none/low	moderate	High
Description	Exclusion from area or rare signs on roadways, no signs in streams.	Occasionally seen on roads and uplands, stream access at 1 or 2 points.	Frequently seen in watershed, multiple stream access points, erosion of stream banks and decreased vegetation noticeable.

Table 3. Observed level of cattle grazing at each site and month sampled as described in table 2.

SITE	TYPE	CATTLE GRAZING LEVEL					
		June 2004	July 2004	Aug 2004	May 2005	June 2005	Aug 2005
IND 1	Burn	1	1	1	0	1	1
IND 2	Burn	1	1	1	0	1	1
Manley	Burn	2	2	2	0	2	2
NFLR 1	Burn	2	2	2	0	2	2
NFLR 2	Burn	2	2	2	0	0	0
IND 3	Control	0	0	0	0	0	0
IND 4	Control	0	0	0	0	0	0
MFLB 1	Control	0	0	0	0	0	0
MFLB 2	Control	0	0	0	0	0	0
MFLB 3	Control	0	0	0	0	0	0

Table 4. Average measured site characteristics for burn and control sites. Standard deviation of summer values in parentheses.

SITE	TYPE	Discharge (L/s)	Mean Temperature (°C)	Maximum Temperature (°C)	Algae: Chlorophyll *a* (mg m^{-2})	Algae: AFDM (mg m^{-2})	Canopy Cover (%)
IND 1	Burn	2.0 (1.7)	10.6 (2.4)	17.8 (4.3)	18.4 (5.5)	4180 (331)	37 (5)
IND 2	Burn	2.3 (2.1)	10.4 (3.0)	20.2 (3.0)	28.7 (12.1)	5530 (3500)	42 (20)
Manley	Burn	1.2 (1.0)	10.9 (2.4)	17.3 (2.4)	59.1 (39.4)	5140 (1440)	31 (2)
NFLR 1	Burn	1.2 (0.8)	10.1 (2.3)	17.0 (4.1)	45.6 (14.2)	19100 (12600)	37 (1)
NFLR 2	Burn	1.4 (1.8)	10.5 (3.2)	17.6 (6.0)	15.6 (12.1)	4920 (4150)	34 (8)
IND 3	Control	4.0 (4.4)	9.5 (2.4)	11.9 (1.6)	33.3 (4.9)	7200 (4320)	84 (3)
IND 4	Control	4.2 (5.6)	8.3 (2.2)	10.2 (1.9)	23.4 (11.2)	5820 (398)	91(2)
MFLB 1	Control	1.6 (1.7)	9.1 (2.8)	16.9 (4.6)	65.4 (48.2)	7050 (4090)	81 (0)
MFLB 2	Control	2.1 (2.0)	8.7 (1.5)	10.1 (1.7)	134.0 (92.0)	9450 (3540)	87 (2)
MFLB 3	Control	0.8 (0.8)	10.0 (3.1)	14.4 (3.6)	29.5 (2.3)	5600 (2830)	64 (2)
Mean	Burn	1.6	10.5	18.0	33.5	7780	36
	Control	2.6	9.1	12.7	57.1	7020	81

Table 5. Total taxa richness for burned and control sites in 2004 and 2005 for each sample type. Taxa were counted at the lowest level of taxonomic detail possible, usually family or genus; higher levels were not counted when lower levels were present. Other includes primarily: Ostracoda, Copepoda, Oligochaeta, Gordioidea, Arachnid and Hymenoptera.

		Taxa Richness					
		DRIFT		BENTHIC		EMERGENCE	
	Order	Burn	Control	Burn	Control	Burn	Control
2004	Coleoptera	9	12	4	6	3	4
	Diptera	14	14	12	10	6	5
	Ephemeroptera	5	5	5	9	1	4
	Hemiptera	3	2	3	1	4	4
	Plecoptera	6	9	10	9	1	4
	Trichoptera	12	13	9	13	1	2
	Other	14	14	13	15	5	6
	TOTAL	63	69	56	63	21	29
2005	Coleoptera	9	10	3	3	7	4
	Diptera	19	19	9	10	6	7
	Ephemeroptera	6	7	5	6	5	4
	Hemiptera	4	3	1	1	5	2
	Plecoptera	13	12	8	9	3	4
	Trichoptera	13	14	11	12	6	6
	Other	13	13	10	13	6	9
	TOTAL	77	78	47	54	38	36

Appendices

Appendix A. Drift taxa correlations (Pearson's r) with Non-Metric Multidimensional Scaling (NMS) axes.

Taxon			Axis 1	2	3
Annelida	Oligocaheta		-0.128	-0.046	0.154
Arachinid					
	Araneae		0.089	-0.008	0.314
	Hydrachnidia		0.099	-0.197	0.434
Coleoptera			-0.089	-0.022	0.25
	Amphizoidae	*Amphizoa*	-0.061	0.127	0.27
	Carabidae		0.057	0.083	0.326
	Chrysomelidae		-0.085	0.023	0.054
	Curculionidae		0.021	0.032	-0.049
	Dytiscidae		-0.224	-0.224	0.287
	Elmidae		-0.088	-0.432	0.136
	Haliplidae		-0.123	0.248	-0.001
	Hydrophilidea		-0.111	-0.003	0.381
	Polyphaga		-0.17	0.127	0.346
	Ptiliidae		0.231	0.197	-0.005
	Staphylinidae		-0.145	0.015	0.388
Collembola					
	Isotomidae		-0.272	0.115	0.371
	Sminthuridae		-0.213	0.193	0.389
Crustacea					
	Copepoda		-0.106	0.006	0.443
	Ostracoda		-0.247	0.052	0.142
Diptera					
	Athericidae	*Atherix*	0.023	0.037	0.309
	Ceratopogonidae		-0.341	-0.018	0.092
		Atrichopogon	-0.181	0.152	-0.121
		Forciponyia	-0.115	-0.091	0.119
	Chironomidae		-0.837	-0.101	0.406
	Dixidae		-0.224	-0.104	0.449
		Dixa	-0.485	-0.594	0.122
		Meringedixa	-0.302	-0.254	0.283
	Dolichopodidae		-0.168	-0.192	0.106
	Empididae		-0.406	-0.026	0.022
	Muscidae		-0.305	0.076	-0.128
	Pelecorhynchidae	*Glutops*	-0.176	0.132	-0.185
	Psychodidae		-0.209	-0.19	0.299
		Pericoma	-0.047	0.053	-0.112
	Simuliidae		-0.544	-0.038	0.107

		Prosimulium	0.012	-0.078	-0.202
	Stratiomyidae		-0.134	0.229	-0.131
	Tabanidae		-0.102	0.301	0.064
	Tipulidae		-0.185	0.302	0.004
		Dicranota	-0.244	-0.116	-0.08
		Prionocera	-0.035	-0.07	-0.173
		Tipula	-0.019	-0.033	-0.138
	Other aquatic larvae		-0.614	0.023	0.122
	Brachycera (adults)		-0.016	0.119	0.255
	Nematocera (adults		-0.52	-0.238	0.261
Ephemeroptera			0.051	-0.031	-0.184
	Ameletidae	*Ameletus*	-0.074	-0.409	0.311
	Baetidae	*Baetis*	-0.567	-0.52	0.157
	Ephemerellidae		-0.243	-0.471	-0.043
		Drunella	0.337	-0.178	-0.435
	Heptageniidae		0.399	-0.227	0.22
		Cinygmula	0.141	-0.088	-0.262
		Epeorus	0.244	-0.292	-0.137
	Leptophlebiidae		-0.147	-0.301	0.304
Hemiptera			0.035	0.046	0.17
	Aphididae		-0.355	0.022	0.142
	Macrovellidae		-0.179	0.075	0.185
	Saldidae		-0.382	0.025	0.184
	Homoptera		-0.268	0.246	-0.133
Hymenoptera			-0.353	0.053	0.553
Lepidoptera			0.02	0.022	-0.294
Mollusca					
	Bivalvia		-0.012	0.188	0.218
	Gastropoda		0.156	0.055	0.109
Nematoda			-0.102	0.001	0.368
Nematomorpha	Gordioidea		0.093	0.252	0.341
Plecoptera			-0.017	0.066	0.389
	Capniidae		0.169	-0.303	-0.123
	Chloroperlidae		0.356	-0.245	0.312
		Paraperla	0.224	-0.18	0.007
		Suwallia	0.197	0.014	-0.379
	Leuctridae		0.143	-0.103	0.298
	Nemouridae		-0.002	-0.109	0.49
		Malenka	0.276	0.232	-0.075
		Podmosta	0.163	-0.039	-0.295
		Zapada	-0.371	-0.524	0.02
	Peltoperlidae		0.187	-0.085	0.527
		Yoraperla	0.146	-0.59	0.077

	Perlidae		0.151	-0.142	-0.141
	Perlodidae		0.335	-0.399	0.225
		Isoperla	0.201	-0.058	-0.351
		Setvena	0.042	-0.397	0.024
Terrestrial insects			-0.019	-0.003	0.448
Thysanoptera			-0.351	-0.161	0.262
Trichoptera			-0.042	-0.127	0.364
	Apataniidae	*Allomyia*	-0.314	-0.043	0.066
	Hydropsychidae		0.168	0.295	-0.072
		Parasyche	-0.036	0.039	0.267
	Lepidostomatidae	*Lepidostoma*	0.493	0.214	-0.374
	Limnephilidae		0.329	-0.202	0.312
		Chyranda	0.434	0.04	-0.53
		Clostoeca	0.133	-0.146	0.092
		Cryptochia	0.095	-0.282	0.021
		Dicosmoecus	0.006	-0.204	-0.088
		Eocosmoecus	0.31	-0.329	-0.008
		Homophylax	0.063	-0.116	-0.205
		Psychoglypha	0.273	0.013	-0.271
	Philopotamidae		0.03	-0.17	-0.159
	Polycentropodidae	*Polycentropus*	0.259	-0.112	-0.125
	Rhyacophilidae	*Rhyacophila*	0.471	0.027	-0.217
	Uenoidae		0.059	-0.014	0.182
		Neophylax	-0.109	-0.032	-0.093
Turbellaria			0.279	-0.079	0.671

Appendix B. Benthic taxa correlations (Pearson's r) with Non-Metric Multidimensional Scaling (NMS) axes.

TAXA			Axis 1	2	3
Annelida	Oligocaheta		0.431	0.009	0.551
Arachinid	Araneae		-0.341	-0.043	-0.203
	Hydrachnidia		-0.788	-0.111	-0.327
Coleoptera			0.357	0.476	0.232
	Dytiscidae		-0.203	0.199	-0.02
	Elmidae		-0.453	-0.193	0.076
	Hydrophilidea		-0.154	-0.14	-0.233
	Staphylinidae		-0.107	0.001	0.003
Collembola	Isotomidae		-0.241	0.288	0.042
	Sminthuridae		-0.096	0.078	0.311
Crustacea	Amphidod		-0.024	-0.015	0.148
	Copepoda		-0.514	-0.236	-0.262
	Ostracoda		-0.671	-0.281	-0.477
Diptera					
	Ceratopogonidae		-0.397	-0.11	-0.082
	Chironomidae		-0.362	-0.798	-0.668
	Dixidae		-0.271	-0.121	-0.272
		Dixa	-0.28	-0.17	-0.4
		Meringedixa	0.19	0.441	-0.045
	Empididae		0.1	-0.471	-0.346
	Muscidae		0.079	-0.038	0.071
	Pelecorhynchidae	*Glutops*	-0.26	0.257	0.359
	Psychodidae		-0.524	0.062	-0.155
	Simuliidae		0.371	-0.573	-0.212
		Prosimulium	0.067	0.505	0.327
	Stratiomyidae		-0.019	-0.201	-0.232
	Tabanidae		0.346	-0.068	0.081
	Tipulidae		-0.122	-0.246	-0.269
		Dicranota	-0.191	-0.431	-0.36
	Brachycera (adults)		0.151	-0.463	-0.412
	Nematocera (adults)		-0.132	-0.27	-0.381
Ephemeroptera			0.07	0.04	0.34
	Ameletidae	*Ameletus*	-0.532	-0.191	0.231
	Baetidae	*Baetis*	-0.285	-0.653	-0.625
	Ephemerellidae		-0.405	-0.438	-0.42

	Ephemerellidae	*Drunella*	0.12	0.102	0.524
	Heptageniidae		-0.771	-0.341	-0.537
	Heptageniidae	*Cinygma*	0.026	0.17	0.169
	Heptageniidae	*Cinygmula*	0.014	0.369	0.689
	Heptageniidae	*Epeorus*	0.037	0.229	0.566
	Leptophlebiidae		-0.15	-0.139	0.001
Hemiptera			-0.09	0.11	0.046
	Aphididae		0.129	0.163	0.098
	Homoptera		-0.16	-0.177	-0.255
Hymenoptera	Hymenoptera		-0.323	-0.317	-0.552
Mollusca	Gastropod		-0.322	0.088	-0.118
	Sphaeriidae		-0.144	-0.021	-0.027
Nematoda			0.121	-0.169	0.117
Nematomorpha	Gordioidea		0.095	0.205	0.347
Plecoptera			0.047	-0.035	0.431
	Capniidae		-0.27	0.166	0.246
	Chloroperlidae		-0.771	-0.152	-0.248
		Paraperla	0.102	0.143	0.527
	Leuctridae		-0.363	0.039	-0.038
	Nemouridae		-0.558	-0.42	-0.607
		Malenka	0.549	-0.038	0.203
		Visoka	0.034	-0.141	0.287
		Zapada	-0.095	-0.222	0.012
	Peltoperlidae		0.075	0.304	0.114
		Yoraperla	-0.71	-0.124	-0.003
	Perlidae		-0.228	-0.212	-0.116
		Doroneuria	-0.008	-0.212	0.06
	Perlodidae		-0.733	-0.322	-0.204
		Isoperla	0.011	0.173	0.165
		Setvena	0.162	-0.215	0.049
Terrestrial insects			-0.118	0.022	0.256
Thysanoptera			-0.522	-0.371	-0.598
Trichoptera			-0.159	0.143	0.345
	Apataniidae	*Allomyia*	0.251	-0.141	-0.167
	Glossosomatidae	*Anagapetus*	0.018	0.087	0.249
	Hydropsychidae		-0.069	0.116	-0.284
		Parasyche	0.352	0.023	0.293
	Lepidostomatidae	*Lepidostoma*	0.272	0.196	0.638
	Limnephilidae		-0.544	-0.281	-0.154
		Chyranda	0.156	0.195	0.677
		Cryptochia	-0.459	-0.236	-0.188

		Eocosmoecus	-0.076	-0.202	0.091
		Homophylax	0.396	0.199	-0.112
		Psychoglypha	-0.029	0.152	0.209
	Philopotamidae		-0.324	-0.156	-0.213
		Dolophilodes	0.317	0.047	0.279
	Polycentropodidae	*Polycentropus*	0.184	-0.045	0.24
	Rhyacophilidae	*Rhyacophila*	-0.416	-0.042	0.142
	Uenoidae		-0.074	-0.149	-0.186
		Neophylax	0.405	-0.188	0.348
Turbellaria			0.579	-0.161	0.445

Appendix C. Emergence taxa correlations (Pearson's r) with Non-Metric Multidimensional Scaling (NMS) axes.

			Axis		
TAXA			1	2	3
Arachinid	Araneae		-0.113	-0.011	0.635
	Hydrachnidia		-0.501	0.44	0.087
Coleoptera			-0.138	-0.041	0.277
	Hydrophilidea		-0.071	-0.111	0.241
	Carabidae		0.226	-0.226	0.255
	Curculionidae		-0.32	-0.166	0.035
	Staphylinidae		-0.287	-0.258	0.285
	Ptiliidae		-0.157	-0.358	-0.013
Collembola	Isotomidae		-0.436	0.313	0.065
	Sminthuridae		-0.445	0.213	-0.082
Diptera			-0.329	0.017	0.19
	Ceratopogonidae		-0.495	-0.308	0.359
	Chironomidae		0.085	-0.583	0.634
	Dixidae		-0.358	-0.326	0.175
	Psychodidae		-0.447	-0.012	-0.013
	Simuliidae		-0.18	-0.232	0.379
	Tipulidae		-0.039	-0.34	0.417
	Brachycera (adults)		-0.252	-0.627	0.411
	Nematocera (adults		-0.034	-0.064	0.332
Ephemeroptera			0.283	0.116	0.245
	Ameletidae	*Ameletus*	-0.147	0.214	0.121
	Baetidae		-0.08	-0.45	-0.34
	Ephemerellidae		-0.292	-0.036	-0.245
	Heptageniidae		-0.344	0.024	-0.081
Hemiptera	Hemiptera		-0.196	-0.198	0.276
		Hebridae	0.037	-0.107	0.271
		Macrovellidae	0.082	-0.225	0.232
		Notonectidae	0.097	0.118	0.268
		Saldidae	-0.016	0.018	0.243
		Homopter	-0.316	-0.159	0.032
		Aphidida	-0.471	-0.331	-0.24
Hymenoptera			-0.383	-0.327	0.696
Lepidoptera			-0.255	-0.137	0.108
Plecoptera			0.191	0.174	0.223
	Capniidae		-0.062	-0.106	0.05
	Chloroperlidae		-0.376	-0.04	-0.341
	Nemouridae		-0.238	-0.148	-0.149
	Perlodidae		-0.211	0.174	0.021

Trichoptera			0.021	0.203	0.465
	Glossosomatidae		-0.365	-0.035	-0.046
	Hydropsychidae		-0.245	0.026	-0.061
	Lepidostomatidae	*Lepidostoma*	-0.201	-0.04	0.092
	Limnephilidae		-0.422	-0.067	0.031
	Philopotamidae		-0.291	-0.071	0.045
	Rhyacophilidae	*Rhyacophila*	-0.268	-0.218	-0.041
Thysanoptera			-0.335	-0.245	0.209

Appendix D. Metadata for raw data available from the US Forest Service Pacific Northwest Research Station, Wenatchee Washington.

TAXA LIST	
Taxa Code	Unique code to identify taxa. Uses first 2 letters of Order, Family, Genus and Species to the level it was identified to. A 3rd letter was used if necessary to make the code unique. The last letter of A, L or P signifies life stage; adult, larvae or pupae.
Phylum	
Class	
Order	
Family	
Genus	
Species	
Life stage	Larvae, adult or pupae.
a	Value for a in biomass equations of the form DM = a * (L^b); where DM = dry mass in mg and L = length in mm.
b	Value for b in biomass equations of the form DM = a * (L^b); where DM = dry mass in mg and L = length in mm.
Feeding group	Functional feeding group as classified by Merritt and Cummins (1996).
Life history	Unvioltine, multivoltine or semivoltine as classified by Merritt and Cummins (1996).
Habitat	
aquatic	True for aquatic, false for terrestrial. Terrestrial adults of aquatic larvae are categorized as terrestrial.

Benthic Data	
Site Code	Unique code for each study site as shown in Figure 1..
Date	Month and Year sample was taken.
Site Type	Burn or Control.
Taxa Code	Unique code for each taxa as described in Taxa List metadata.
Total	Number of individual invertebrates collected at each site and sampling period..
Number per m^2	Number of individuals corrected for area sampled.
Biomass (mg)	Total invertebrate biomass based on length measurements and regression equations.
mg per m^2	Biomass corrected for area sampled.

Drift Data	
Site Code	Unique code for each study site as shown in Figure 1.
Date	Month and Year sample was taken.
Site Type	Burn or Control.
Taxa Code	Unique code for each taxa as described in Taxa List metadata.
Total	Number of individuals collected in each drift net at each sampling period.
Number per m^3	Number of individuals corrected for discharge through drift net and time the net was left out.
Biomass (mg)	Total invertebrate biomass collected in each drift net based on length measurements and regression equations.
mg per m^3	Biomass corrected for discharge through drift net and time net was left out.

Emergence Data	
Site Code	Unique code for each study site as shown in Figure 1.
Date	Month and Year sample was taken.
Site Type	Burn or Control.
Taxa Code	Unique code for each taxa as described in Taxa List metadata.
Total	Number of individuals collected at each site and sampling period.
Number per m^2 per hour	Number of individuals corrected for area sampled and time traps were left out.
Biomass (mg)	Total invertebrate biomass based on length measurements and regression equations.
mg per m^2 per hr	Biomass corrected for area sampled and time traps were left out.

Sample Info	
Site Code	Unique code for each study site as shown in Figure 1.
Sample Type	Benthic, drift or emergence sample.
Date	Month and Year sample was collected.
Time out (hr)	For drift and emergence samples, number of hours that nets were left out.
Sample area	For benthic and emergence samples, m^2 of stream sampled. For drift samples, discharge m^3 per hour through drift net.

Algae	
Site Code	Unique code for each study site as shown in Figure 1.
Site Type	Burn or Control.
Sample Date	Month sample was collected. All algae samples were collected in 2005.
Chlorophyll *a*	mg chlorophyll *a* per m^2 of substrate.
AFDM	Ash free dry mass of algae per m^2 of substrate.

Temperature	Excel spreadsheet with worksheet for each site.
Date/Time	Date and time temperature was recorded. Temperatures were recorded hourly.
Temperature (°C)	Temperature in degrees Celsius.
Date	Date temperature was recorded.